THE IMPACT OF WEATHER ON THE BEHAVIOR AND ECOLOGY OF BIRDS

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THE IMPACT OF WEATHER ON THE BEHAVIOR AND ECOLOGY OF BIRDS

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EDITORIAL
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Editorial: The Impact of Weather on the Behavior and Ecology of Birds

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Editorial on the Research Topic

The Impact of Weather on the Behavior and Ecology of Birds

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INTRODUCTION

In recent times, research examining the effect of weather on birds has focused predominantly on the impact of climate change (Crick, 2004; Dunn and Winkler, 2010; Şekercioğlu et al., 2012; Riddell et al., 2021) or extreme weather events (e.g., Easterling et al., 2000; Bailey et al., 2017), often overlooking the fact that even small-scale variation in weather conditions can affect almost every aspect of avian biology. Short-term or localised changes in temperature, rainfall and wind can strongly influence individual behaviour, life history, physiology and morphology, with consequences at the population and species levels (e.g., McGowan et al., 2004; Wiley and Ridley, 2016). Further study of these processes is likely to play a key role in shaping our understanding of the mechanisms by which birds respond to climate change, but also has broader implications across ecology, evolution and conservation.

Birds are an ideal group in which to investigate the effects of weather because they occur in almost every ecosystem across the globe, they exploit a wide variety of food resources, and thousands of bird species migrate between vastly different environments during the course of their annual life cycle (Elkins, 1983; Both et al., 2006; Gordo, 2007). This Research Topic brings together articles from researchers across the globe who take a range of approaches to advance our understanding of the impact of weather on birds. The contributions take the form of original research papers, review papers that synthesise our understanding of topical issues or perspectives that highlight issues warranting further research attention. The articles cover three main aspects: (1) the influence of weather on birds during nest building and incubation; (2) the influence of weather on birds during offspring growth; and (3) the impact of weather on birds during the non-breeding season.

IMPACT OF WEATHER ON BIRDS DURING NEST BUILDING AND INCUBATION

Weather conditions impact the breeding ecology of birds, but a disproportionate amount of research attention has focused on the impacts of temperature rather than other weather variables, such as rainfall. Yet, rainfall impacts birds by influencing where (Fogarty et al., 2020) and when (Hidalgo et al., 2019) they breed. Rainfall also affects their reproductive output (Rodríguez and Bustamante, 2003; Skagen and Adams, 2012), for example by determining the foraging success of parents (Dawson and Bortolotti, 2000; Öberg et al., 2015). This Research Topic highlights that rainfall impacts birds in diverse ways, and Rosamond et al. show that Dickcissel (*Spiza americana*) populations decline with increasing amounts of summer rainfall. However, drought also influences the distribution of breeding birds (Barbaree et al., 2020; Campos-Cerqueira and Aide, 2021) and particularly so in arid regions (Herremans, 2004). Bourne et al. advance our understanding of adaptive responses to drought by showing that Southern Pied Babblers (*Turdoides bicolor*) in the Kalahari Desert in South Africa significantly reduce their reproductive effort during breeding seasons characterised by drought but subsequently increase their reproductive effort during the breeding seasons immediately following droughts. Birds may therefore adapt to drought by delaying their reproduction until the dry conditions have passed, and such lagged effects of weather conditions certainly deserve further attention.

The nest building and incubation stages of reproduction have lagged behind the offspring rearing stage in terms of the amount of research attention they have received (Hansell, 2000). Yet, it is now agreed that creating suitable microclimates in which to incubate eggs is important for embryos because temperatures that are higher or lower than optimal result in the mortality and suboptimal development of the embryos, respectively (McGowan et al., 2004; DuRant et al., 2012, 2013). In this Research Topic, we address this imbalance in research effort with a number of articles focusing on the nest and egg stages of reproduction. Specifically, Lowney et al. show that the extremely large communal nests of Sociable Weavers (*Philetairus socius*) provide year-round protection from adverse weather conditions in South Africa, whilst Perez et al. provide a comprehensive review of the influence of weather conditions on the morphology of birds' nests.

Other studies in the Research Topic address the effects of weather on breeding phenology. Hoover and Schelsky and McGuire et al. show that Prothonotary Warblers (*Protonotaria citrea*) and Arctic breeding waders, respectively, lay eggs earlier in warmer springs. Further, Huchler et al. show that the link between temperature and egg-laying phenology varies with the degree of urbanisation in Eurasian Kestrels (*Falco tinnunculus*), whilst Bründl et al. show that the link between temperature and phenology varies with altitude in Blue Tits (*Cyanistes caeruleus*). Nilsson et al. examine the influence of fine-scale variation in weather conditions on fecundity and show that White-throated Dippers (*Cinclus cinclus*) lay smaller clutch sizes in warmer temperatures. Elsewhere, Higgot et al. show that the incubation periods of Long-tailed Tits (*Aegithalos caudatus*) were longer in summers with higher amounts of rainfall. The amount of rainfall is expected to change over time (Trenberth et al., 2003) and so this study helps us better understand the impacts of rainfall on birds in a changing climate.

IMPACT OF WEATHER ON BIRDS DURING OFFSPRING GROWTH

Weather conditions impact the growth of offspring (Mainwaring and Hartley, 2016), both directly via effects on cooling the young (Ardia et al., 2010) and indirectly by influencing the provisioning behaviours of the parents (Wiley and Ridley, 2016; Nord and Nilsson, 2019). In this Research Topic, Sauve et al. provide a comprehensive review of these processes and suggest ways to improve evolutionary predictions, whilst de Zwaan et al. show contrasting effects of weather on growth in three alpine songbirds. Finally, Andreasson et al. highlight those issues that require further research attention if we are to increase our understanding of the impact of temperature on offspring growth. This is important because negative impacts experienced during growth often have long-lasting effects on individuals through to adulthood (Nord and Giroud, 2020).

IMPACT OF WEATHER ON BIRDS DURING THE NON-BREEDING SEASON

Birds are also impacted by weather during the non-breeding season and on migration. Those species living at high latitudes in the northern hemisphere may struggle to survive the cold winter months (Haftorn, 1972; Wolf and Hainesworth, 1972; Spencer, 1982), when the short, cold days barely provide sufficient time for small birds to forage and acquire enough energy to avoid starvation, and the low temperatures increase the energetic cost of staying warm (Brodin, 2007; Krams et al., 2010). Whilst some passerines save energy by occupying cavities that provide them with shelter from the cold night sky (Mainwaring, 2011), Boyer and MacDougall-Shackleton show experimentally that White-throated Sparrows (*Zonotrichia albicollis*) increased their fat levels in response to exposure to a hypobaric climatic wind tunnel that simulated winter storms.

Migratory species are susceptible to changing weather conditions at multiple stages of their journey and must time their movements accordingly (Haest et al., 2020). Here, Carneiro et al. examine the migratory behaviour of Whimbrels (*Numenius phaeopus islandicus*) in relation to temperature and winds, and Manola et al. use radar data to examine the intensity of migration over the North Sea in relation to synoptic weather conditions. Intense nights of migration were associated with an absence of rainfall and the presence of strong tailwinds, illustrating that sophisticated technological approaches can be used to examine the migratory behaviour of birds at large spatial scales.

CONCLUSIONS

The papers included in this Research Topic describe studies performed on several continents and increase our understanding of the impacts of weather on birds. We have included papers that explore exciting new topics such as the linkages between weather and the phenology of birds along gradients of urbanisation, the lagged effects of weather upon breeding birds and how birds may mitigate the negative impacts of drought by delaying their reproduction until the following breeding season. These studies have implications for our understanding of climate change because we can only accurately predict how birds may be affected by change if we have a sound understanding of how they are impacted by more typical weather conditions. We hope that the papers included in this Research Topic will spur many further studies that increase our understanding of the impact of weather on the behaviour and ecology of birds.

AUTHOR CONTRIBUTIONS

MM drafted the editorial. AN and SS edited the draft. All authors approved the final version for publication.

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Linking Weather and Phenology to Stopover Dynamics of a Long-Distance Migrant

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For many migratory species, migration can represent a significant part of the annual cycle and the strategies used to move between the breeding and non-breeding areas vary considerably. Weather conditions are important during migration, particularly wind and temperature, and can play a crucial role in the timing of events during the annual cycle of migratory birds. When timing of specific events is important, for example spring arrival and laying dates, the effects of weather on the previous migration might lead to important fitness consequences, as it may alter migration speed. During spring, Icelandic whimbrels *Numenius phaeopus islandicus* display two main migratory behaviors: a direct flight from the wintering to the breeding sites (direct migration), or, more commonly, two flights with one stopover (stopover migration). We investigated how wind conditions, temperature and spring departure date may drive individuals to adopt either migratory behavior. Interestingly, we found no differences in wind support during migratory flights, in temperature closer to Iceland or on crosswinds experienced in the region before reaching the main stopover areas. However, when individuals undertook a direct flight, departure date from the wintering sites was on average later, but this was not explained by wind patterns over a period of 7 days prior to departure. In addition, we explored the variation at the individual level for three birds that changed migratory behavior between years. The differences in all variables for these individuals reflected the variation observed at the population level. Overall, in such long migrations, it seems advantageous to perform a shorter flight to a stopover area, from where the weather conditions in the breeding areas may be assessed and avoid the risk of facing stochastic inclement weather prior to breeding, while synchronizing time of arrival with conspecifics. In contrast, direct flights seem more common when individuals are time pressed.

Keywords: *Numenius phaeopus*, whimbrel, migration, migration strategy, wind, wader, shorebird, flight behavior

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INTRODUCTION

Migration can represent a significant part of an individual annual cycle and the strategies used to move between the breeding and non-breeding areas vary considerably (Newton, 2007; Hansson and Åkesson, 2014). Animals may take advantage of the flow of the medium where they move to support migration (e.g., air or water; Chapman et al., 2011) and optimal bird migration theory postulates that energy or time costs should be kept at a minimum (Alerstam and Lindström, 1990).

Hence, weather conditions are often taken into consideration during migration, particularly wind and temperature, as these parameters have been shown to influence migration at different stages and in different ways (Liechti, 2006; Shamoun-Baranes et al., 2017). During migratory flight, wind can be favorable but also cause birds to extend the length of migration (Gill et al., 2014), drift due to crosswinds (Grönroos et al., 2013; Horton et al., 2016) or even force stops (Shamoun-Baranes et al., 2010; Klaassen et al., 2017); the effect of temperature on flight has been studied to less extent, but it has been shown to influence individuals' flight altitude (Senner et al., 2018). At stationary locations (e.g., during wintering or stopover), individuals can either select favorable winds at departure (Schaub et al., 2004; Gill et al., 2014), or depart regardless of wind conditions (Thorup et al., 2006), and this can be context dependent (e.g., depending on subsequent flight length, season and migratory strategy; Dierschke and Delingat, 2001; Schmaljohann et al., 2012; Packmor et al., 2020); additionally, temperature can also influence the decision of when to initiate the migratory flight (Schmaljohann et al., 2013; Berchtold et al., 2017). Besides extrinsic factors, migratory behavior can be shaped by individual condition too. For example, individual fuel reserves at departure can influence where to stop next (Anderson et al., 2019), and departure probability can result from an interaction of fuel load and wind conditions (Arizaga et al., 2011). Weather can therefore play an important role on the annual cycle of migratory birds and changes in the atmospheric patterns at a large scale may influence whole populations or species, through costs of energy and time during migration (La Sorte and Fink, 2017; La Sorte et al., 2018). Understanding the mechanisms shaping migratory behavior can thus help predicting how these species will respond to variation in weather patterns.

When the timing of specific annual events is relevant for individual fitness, such as the timing of breeding (Perrins, 1970; Drent, 2006), the effect of weather during spring migration might have important consequences, as it can alter migration speed (Alerstam and Gudmundsson, 1999; Shamoun-Baranes et al., 2010). For example, if an individual encounters unfavorable weather conditions during spring migration, it may increase the duration of migration, leading to latter arrival at the breeding grounds, later breeding and ultimately result in lower breeding success than conspecifics breeding earlier (Drake et al., 2014). Therefore, it might be expected that birds will select the best wind support at departure so that at least the initial stages of migratory flight can take advantage of such subsidies. However, if wind conditions during the departure period are stable, the timing of departure should be independent of wind (Weber and Hedenström, 2000). In addition, there can be particular risks associated with long flights over unsuitable habitat for landing or feeding. Unfavorable weather conditions encountered *en route* may lead to higher energy expenditure, increasing the probability of depleting fuel stores before a suitable location for stopping is within reach and, in extreme conditions, result in mortality (Newton, 2006).

Icelandic whimbrels *Numenius phaeopus islandicus* typically complete their annual migrations in two or three flights (Alves et al., 2016; Carneiro et al., 2019a). After breeding in Iceland, autumn migration is commonly completed in one flight over open waters to the wintering sites, which are mostly located in West Africa. During spring, however, two main migratory behaviors have been identified, regarding route and number of stopovers: a direct migration, where whimbrels again fly non-stop to Iceland, and a stopover migration, where individuals travel first to a stopover site (usually in Britain and Ireland) and then fly to the breeding sites (7–17 days later; Carneiro et al., 2019a). Hence, these two migratory behaviors differ in travel duration from the winter sites to Iceland, but also in the timing of arrival at the breeding sites, with direct migrants arriving earlier than those undertaking a stopover (*unpublished data*). Arriving early to a region where favorable breeding conditions are available for a relatively short period can be important, as it may increase the probability of successful reproduction (Morrison et al., 2019). In fact, in Icelandic whimbrels, fledging success decreases with laying date (*submitted*). Despite this, stopover migration is more common, occurring in 80% of occasions (Carneiro et al., 2019a).

Here, we explore how wind conditions, temperature and departure date from winter location relate to the spring migratory behavior (direct vs. stopover) of Icelandic whimbrels. We envisage two non-mutually exclusive scenarios: (i) whimbrels adjust migratory behavior during flight, depending on conditions experienced *en route* up to the suitable stopover locations; (ii) make migratory decisions prior to departure, given local (weather) conditions. In order to assess the first hypothesis, we define a "decision latitude" where birds might change overall direction of migration, and test if wind support experienced until this latitude and the temperature at this latitude differs between individuals taking a direct or a stopover route. Additionally, we compare the zonal (longitudinal) wind conditions experienced between migratory behaviors when individuals approach the main stopover region. We expect that wind conditions experienced *en route* will be more favorable (e.g., more wind support, weak westerlies) and/or temperature higher when individuals perform a direct migration, as fuel reserves should be higher, and temperature can act as a cue that conditions in Iceland are likely to be favorable upon arrival. To investigate if migratory behavior is defined prior to departure, we test the role of departure date from the wintering sites, and the influence of wind support at this stage. Given previous evidence, we expect departure date to differ between migratory behaviors, and that whimbrel's selection for wind support shall depend on the variability of wind conditions during the departure period (Weber and Hedenström, 2000; Thorup et al., 2006). In addition, using three repeatedly tracked birds that changed migratory behaviors over the years, we explore how individual level variation compares to population level variation on the factors mentioned above.

MATERIALS AND METHODS

From 2012 to 2018, adult whimbrels were caught on the nest, in the southern lowlands of Iceland (63.8°N; 20.2°W), using a spring trap (Moudry TR60[1]). Each bird was fitted with a combination of color rings and a geolocator attached to a leg flag (model Intigeo-W65A9RJ from 2012 to 2014 and Intigeo-C65 since; Migrate Technology Ltd.). Tagged individuals were caught using the same technique one or more years later in order to retrieve and replace the devices, allowing repeated tracking over the years. We deployed a total of 138 geolocators, and retrieved 66, from 39 individuals, despite the return rate to the breeding areas being higher (*unpublished data*). One device was damaged and contained no data, another stopped recording shortly after departure from Iceland, and a third in mid-winter. Bird sex was determined using biometrics following Katrínardóttir et al. (2013; n = 24), molecularly (as in Katrínardóttir et al., 2013; n = 9) or through behavioral observation (copulating position, assuming that males were on top; n = 3). In order to estimate geographical locations, light data recorded by the geolocators was analyzed as described in Carneiro et al. (2019a). Given that these data only allow a minimum temporal resolution of 12 h (two locations per day), we used geolocator recorded data on temperature, conductivity and wet contacts (recorded every 4 h) to refine timings of departure and arrival (Battley and Conklin, 2017; see details in Carneiro et al., 2019a). Stopover and winter locations were defined, for each individual and tracked year, as the average of all locations during each period. In five cases, a movement southward was observed at spring departure from the wintering sites. We considered this unlikely and due to geolocation precision errors through shading, and assumed migration from the first position on the track northwards. The location of arrival into Iceland was assumed to be the breeding region (63.8°N, 20.2°W).

Whimbrels are known to migrate in flocks (Piersma et al., 1990; Watts et al., 2017), therefore migratory decisions may or may not be taken independently by a given individual. Geolocator tracks allow individual migratory behavior to be related to phenology and external factors like weather, but migratory decisions such as whether to stopover may be made communally. However, all individuals in a given flock are subject to same external drivers during migration so relating individual movement patterns to external forces remains meaningful.

Temperature and Wind Data

Temperature and wind data were retrieved from the National Centres for Environmental Prediction (NCEP; Kanamitsu et al., 2002), using the R package "RNCEP" (Kemp et al., 2012a). Although bird migration can occur at higher altitudes (e.g., Alerstam and Gudmundsson, 1999), whimbrel flight altitude during migration is unlikely to be higher than 1,500 m above sea level (a. s. l.; Alves et al., 2016, *unpublished data*). Hence, data was retrieved for each location, at the air pressure of 1,000, 925, and 850 hPa, representing altitudes of 111, 762, and 1,457 m above sea level, respectively. In addition, temperature data during the departure period from the stopover site was also retrieved for the surface level.

Based on visual inspection of whimbrel tracks (Carneiro et al., 2019a), we defined a "decision latitude" at 42°N, where individuals might change the overall migration direction and stop, and a "decision window" between 37 and 50°N, i.e., the region before the main stopover locations in Britain and Ireland, where individuals might be influenced and pushed east by zonal winds to make a stopover, as westerlies prevail in this region. Additionally, given the subjectivity of the assumptions above and the error associated with geolocator positional data (ca. 200 km; Phillips et al., 2004; Shaffer et al., 2005; Fudickar et al., 2012), we also considered two more "decision latitudes" at 37 and 47°N. These latitudes are ca. 10% of the average distance between wintering and breeding sites (assuming a great circle route), to the south and north of 42°N. The locations and time when crossing 37, 42, and 47°N were interpolated linearly, assuming constant ground speed.

For all individuals, each location attained during migration, wintering and stopover sites, was annotated with the zonal (u) and meridional (v) wind components. In order to investigate wind support during migratory flight, we calculated the flow assistance (FA) as the tailwind component (Kemp et al., 2012b) and the air-to-ground speed ratio (AGR; Alerstam, 1979; Gill et al., 2014). The distance between positions was calculated as the great circle distance using the function "distCosine" of the R package "geosphere" (Hijmans, 2016). Ground speed was calculated as the speed between consecutive positions during migratory flights, and air speed as the difference of ground speed and the FA component. Hence, when AGR < 1 the individual is experiencing wind support, while AGR > 1 indicates that wind is an impediment to movement. The AGR value at wintering departure for one individual was an outlier (14.05). Since this could have been due to an erroneous location, either at departure or the following one, both locations and associated wind components were removed from further analysis.

Statistical Analysis

We built a generalized linear model (GLM; family binomial) in order to test whether migratory behavior (direct or stopover) varies with mean AGR until 42°N, air temperature at 42°N and departure date from the wintering site, for each air pressure (1,000, 925, and 850 hPa). In addition, we built similar models considering migration until latitudes 37 and 47°N.

In order to test for the influence of wind while crossing the region between 37 and 50°N, we restricted the data to locations within that window and built a GLM (family binomial) with migratory behavior as independent variable and the zonal wind component as explanatory variable, which represents east/west winds. As above, this model was performed for each air pressure (1,000, 925, and 850 hPa). Although variables such as sex, year, and individual may influence spring migratory behavior, these variables were not included in these models as random factors, because sample size limitations (i.e., observations biased toward stopover behavior, that is far more common; Carneiro et al., 2019b) and unbalanced samples across individuals prevented models to converge or led to overdispersion (Harrison et al., 2018). Nevertheless, in order to assess their possible effect, we constructed reduced models for all combinations of each independent and random variable, for migrations until

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[1] www.moudry.cz

42°N and for the region between 37 and 50°N, at the air pressure of 1,000 hPa.

In order to assess if wind support at the wintering site can influence departure date, we retrieved the u and v wind components from NCEP (Kanamitsu et al., 2002; Kemp et al., 2012a), at the same altitudes as above, for the date and location of departure and for each of the previous 7 days (at the same time of the day as the day of departure). Icelandic whimbrels are consistent on departure date from the wintering sites, with a mean individual range of 3.6 days (Carneiro et al., 2019b), hence 7 days (i.e., a period twice as long) were considered to represent the period over which a decision to depart is likely to occur. Then, we calculated AGR and performed a Wilcoxon rank sum test to examine differences between migratory behavior at time of departure. In order to assess if whimbrels select certain wind support at departure, for each migratory behavior we performed a GLM (family binomial) with departure (depart or not) as independent variable and AGR as explanatory variable.

Among the 13 individuals with repeated tracks, only three changed migratory behavior, from direct to stopover. One individual was tracked during two spring migrations, and two individuals were tracked during five spring migrations. Using these data, we further explored individual variation between strategies using the same variables as above. Data were analyzed in software R (R Core Team, 2018) and results are reported as mean ± se, unless otherwise stated.

RESULTS

We compared 9 direct to 48 stopover spring migrations, performed by 36 individuals (16 females and 20 males; **Figure 1**). Stopover sites were located along the Portuguese continental Atlantic coast (*n* = 3), northwest of France (*n* = 4), and Ireland and NW Britain (*n* = 41; **Figure 1**).

For the air pressure levels considered (representing altitudes of 111, 762, and 1,457 m a. s. l.), the mean air-to-ground speed ratio until 42°N and air temperature at that latitude, did not differ for whimbrels undertaking either migratory behavior (**Table 1A** and **Figures 1A**, **2A,B**); but departure date from the wintering sites did, with birds that departed later tending to undertake a direct flight (direct migration: 27 April ± 1.7 days, *n* = 9; stopover migration: 19 April ± 0.6 days, *n* = 48; **Table 1A** and **Figure 2C**). When considering the "decision latitude" at 37°N or at 47°N, the results were similar (**Supplementary Table S1**).

The zonal wind component when crossing the region from latitude 37°N to 50°N was not different between migratory behaviors at any air pressure level considered (**Table 1B** and **Figures 1B**, **2D**), and was predominantly westward (e.g., for 1,000 hPa, direct migration: −1.49 ± 1.52, *n* = 18; stopover migration −3.79 ± 0.70, *n* = 80).

The reduced models provided the same results when considering a possible effect of year or sex on migratory behavior (**Table 1** and **Supplementary Table S2**). However, in a reduced model with departure date as explanatory variable for migratory behavior and individual as random term, we did not find a significant effect (**Supplementary Table S2**), likely due to the low sample size.

Wind support at departure from the wintering sites, measured as AGR at an air pressure of 1,000 hPa did not differ between strategies (Wilcoxon rank sum test: $W = 276$, $p = 0.156$; direct: 1.45 ± 0.15, *n* = 9; stopover: 1.22 ± 0.05, *n* = 47), although it did at higher altitudes, for 925 hPa (Wilcoxon rank sum test: $W = 329$, $p = 0.007$; direct: 1.41 ± 0.15, *n* = 9; stopover: 1.07 ± 0.03, *n* = 47) and 850 hPa (Wilcoxon rank sum test: $W = 352$, $p = 0.001$; direct: 1.22 ± 0.10, *n* = 9; stopover: 0.92 ± 0.03, *n* = 47), being higher (i.e., higher impediment for movement) for birds that flew directly. For each migratory behavior, the AGR at departure and during the previous 7 days had no effect on departure, at any altitude considered, suggesting no or little selection for wind conditions to initiate the flight (**Table 2**).

For the three individuals that changed migratory behavior, from direct to stopover (**Supplementary Figure S2**), the overall pattern of mean AGR, temperature, departure date and zonal winds was similar to that recorded at the population level (**Figures 2E–H**).

DISCUSSION

During spring migration, Icelandic whimbrels display two main migratory behaviors: a direct flight from the wintering to the breeding sites (direct migration), or two flights with one stopover (stopover migration). We investigated how wind conditions, temperature, and spring departure date may drive individuals to adopt each behavior, and found no differences in wind support during migration, on temperature closer to Iceland or on crosswinds experienced in the region before reaching the main stopover sites. However, departure date from the wintering sites was on average later for individuals performing a direct flight to the breeding areas.

Departure date can be influenced by weather conditions, as birds often select favorable winds (Ma et al., 2011; Gill et al., 2014). Long-distance migrating bar-tailed godwits *Limosa lapponica baueri* generally experience favorable conditions during the departure period from the wintering sites, creating few opportunities for wind assistance selectivity. Yet, most off-schedule individuals tend to depart when wind assistance is maximized (Conklin and Battley, 2011). In the case of Icelandic whimbrels, wind conditions at departure were not different between migratory behaviors for 1,000 hPa (i.e., 111 m a. s. l.), suggesting that a direct migratory flight is not taken when wind conditions render more support at low altitudes. However, we found differences at higher altitudes (925 hPa and 850 hPa, i.e., 762 and 1,457 m a. s. l, respectively), in which birds migrating directly would experience more impediment of movement than those performing a stopover. Whimbrels have been observed circling and gaining height at departure from the south coast of Iceland in autumn (TGG pers. obs., but see Piersma et al., 1990), indicating that they may sample the wind conditions at different altitudes. However, it seems unlikely that individuals would sample hundreds of meters above sea level and select worse conditions for a longer migratory flight (i.e., direct to Iceland). A study to determine if, and how high, whimbrels sample wind conditions prior to departure, would help clarify if the differences found here have biological meaning. More

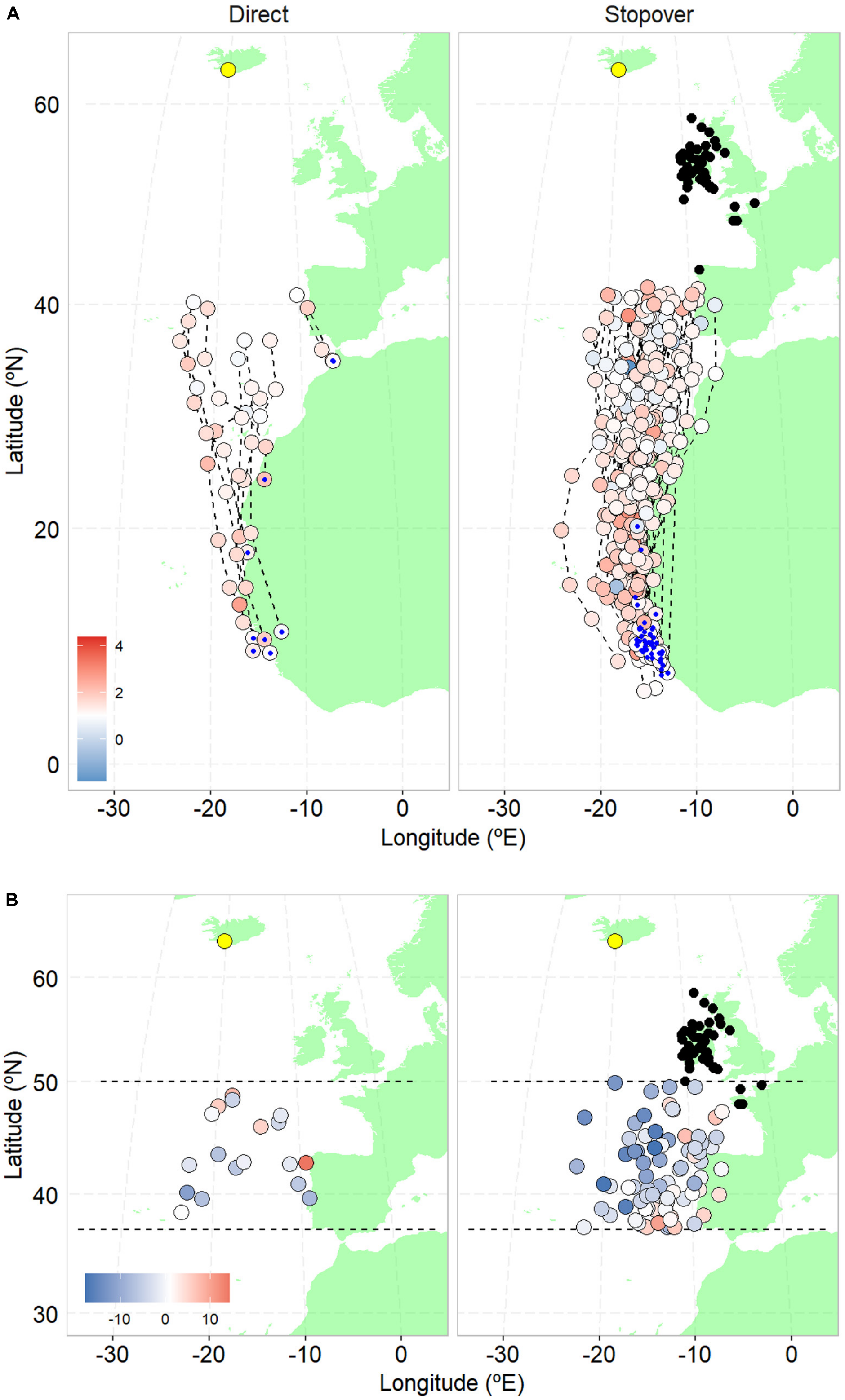

FIGURE 1 | (A) Spring migration locations recorded with geolocators up to latitude 42°N, colored by air-to-ground speed ratio (at 1,000 hPa); blue represents wind support (values below one), whereas red represents wind impediment in the direction of movement (values above one); individual winter locations are given as blue dots. **(B)** Locations during spring migration between latitude 37 and 50°N, colored by zonal wind (u, in ms^{-1}, at 1,000 hPa), where blue (negative) values represent westward winds and red (positive) values eastward winds. Circles depict stopover (black) and breeding (yellow) locations. Left panels show locations of individual whimbrels undertaking a direct migration (*n* = 9), and right panels a stopover migration (*n* = 48).

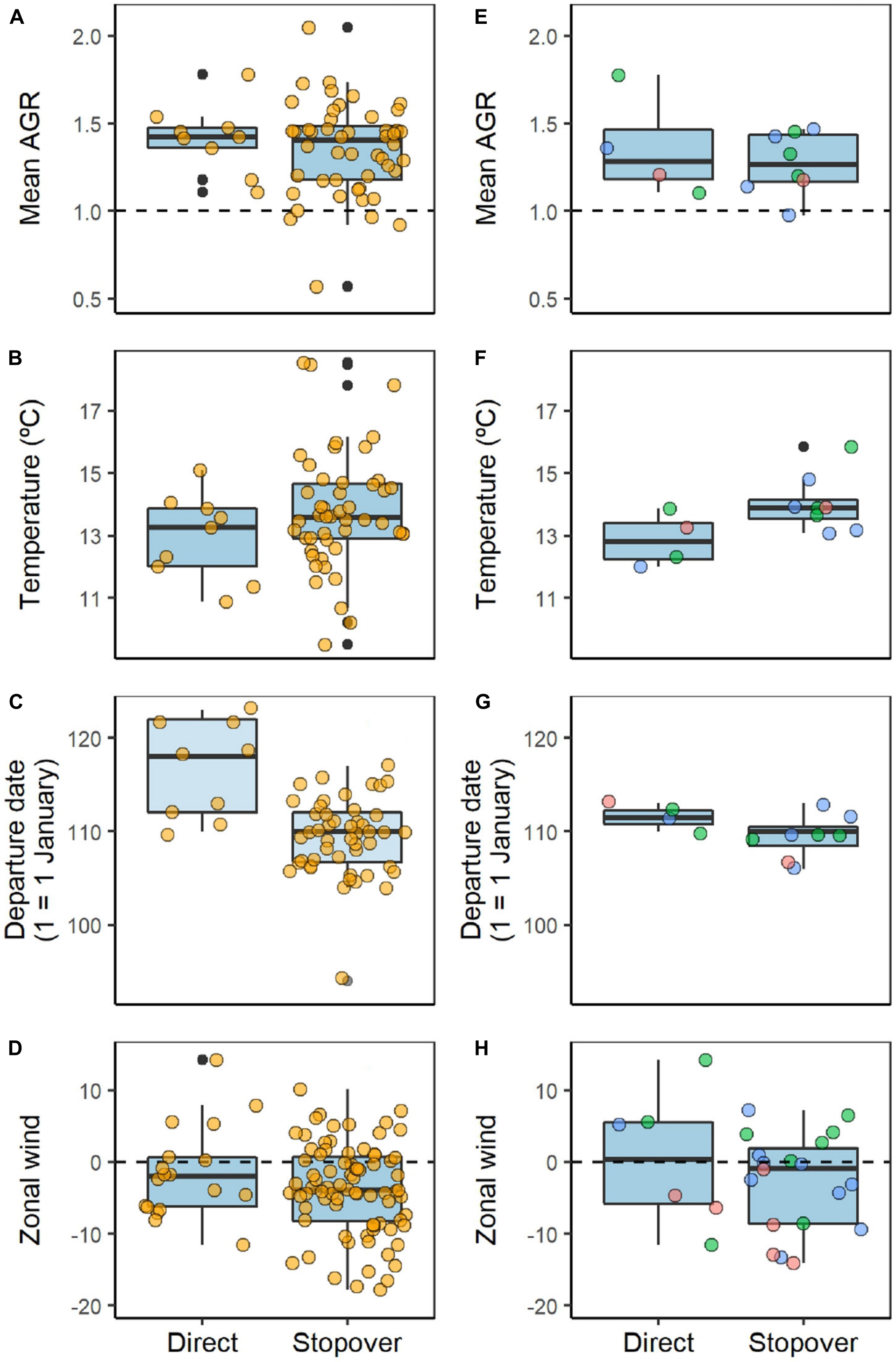

FIGURE 2 | Variation in potential drivers of spring migratory behavior (direct vs. stopover) of Icelandic whimbrels at the population (left column; **A–D**; *n* = 9 direct and 48 stopover migrations), and individual levels (right column, **E–H**). The three individuals that changed spring migratory behavior between years (right column) are coded by color. **(A,E)** Mean individual air-to-ground speed ratio (AGR) from departure up to latitude 42°N (values below one represent wind support, while values above one mean impediment in the direction of movement). **(B,F)** Air temperature experienced by each individual at latitude 42°N. **(C,G)** Departure date from the wintering site. **(D,H)** Zonal wind (u) component, (ms^{-1}) between 37 and 50°N, where negative values represent westward winds and positive values eastward winds (note that between those latitudes the number of locations per track can be more than one, hence the number of locations is higher than the number of migrations; *n* = 18 for direct and *n* = 80 for stopover migrations). All data refers to air pressure 1,000 hPa (i.e., 111 m a. s. l.). Boxplots show the median and 25 and 75% quartiles, whiskers extending up to 1.5 times the inter quartile range from the median and points beyond that are individually marked in black.

TABLE 1 | Generalized linear models testing potential drivers of spring migratory behavior (direct vs. stopover): (A) individual mean air-to-ground speed ratio (AGR) experienced up to crossing 42°N, air temperature at 42°N and departure date from the wintering sites; and (B) zonal wind (east/westward) experienced between 37 and 50°N, for all locations recorded across individuals.

	Air pressure (hPa)		Estimate	SE	*z*	*p*
Migratory behavior *n* = 57 A	1000	Intercept	42.88	15.07	2.85	**0.004**
		Mean AGR	0.27	1.94	0.14	0.891
		Air temperature	0.19	0.31	0.62	0.534
		Departure date	−0.39	0.13	−3.11	**0.002**
	925	Intercept	46.56	14.92	3.12	**0.002**
		Mean AGR	0.21	2.19	0.10	0.925
		Air temperature	0.00	0.19	0.02	0.983
		Departure date	−0.40	0.13	−3.09	**0.002**
	850	Intercept	47.59	14.97	3.18	**0.001**
		Mean AGR	−0.69	2.66	−0.26	0.797
		Air temperature	−0.08	0.14	−0.58	0.563
		Departure date	−0.40	0.13	−2.94	**0.003**
Migratory behavior *n* = 98	1000	Intercept	1.34	0.28	4.83	**<0.001**
		U wind	−0.06	0.04	−1.38	0.168
B	925	Intercept	1.35	0.27	5.02	**<0.001**
		U wind	−0.06	0.04	−1.57	0.116
	850	Intercept	1.43	0.26	5.41	**<0.001**
		U wind	−0.06	0.04	−1.60	0.110

p-values < 0.05 are highlighted in bold.

TABLE 2 | Generalized linear models testing the influence of air-to-ground speed ratio (AGR) at the wintering site, on the departure decision of Icelandic whimbrels undertaking a direct (*n* = 72) or stopover migration (*n* = 376).

Migration	Air pressure (hPa)		Estimate	SE	*z*	*p*
Direct	1000	Intercept	−2.97	1.35	−2.20	**0.03**
		AGR	0.74	0.91	0.81	0.42
	925	Intercept	−3.32	1.15	−2.89	**<0.01**
		AGR	1.05	0.80	1.32	0.19
	850	Intercept	−2.64	1.06	−2.51	**0.01**
		AGR	0.60	0.83	0.73	0.47
Stopover	1000	Intercept	−1.91	0.47	−4.05	**< 0.001**
		AGR	−0.03	0.36	−0.08	0.94
	925	Intercept	−1.66	0.51	−3.26	**< 0.01**
		AGR	−0.27	0.45	−0.59	0.56
	850	Intercept	−1.44	0.54	−2.66	**0.01**
		AGR	−0.54	0.56	−0.96	0.34

p-values < 0.05 are highlighted in bold.

importantly, wind conditions at departure were not different from those recorded during the previous week, and were predominantly unfavorable, suggesting none to low selectivity for wind assistance. However, other factors may also influence the departure decision of individuals, such as the amount of fuel reserves (Sjöberg et al., 2015), temperature (Schmaljohann et al., 2013; Berchtold et al., 2017) and joining a flock of departing conspecifics, which may be important in orientation during flight (Alerstam et al., 1990).

Given the apparent stable conditions departure and the importance of breeding timing in this system (*submitted*), the lack of wind selectivity is not surprising and could explain the direct migration when individuals depart later. By undertaking a direct migration, individuals arrive earlier to the breeding sites in relation to undertaking a stopover (*unpublished data*), which may allow to compensate for a potential delay. However, the laying date does not seem to differ between migratory behaviors (*unpublished data*), suggesting that a direct migration may in fact not always translate into higher breeding success.

If conditions during spring migration flight are not different between migratory behaviors (until the same region of migration) and there are no clear advantages for an early arrival after a direct migration, then why performing a stopover is predominant across this population? The main stopover sites are in Britain and Ireland, which are relatively close to the breeding sites, in Iceland. Hence, individuals might be able to assess the weather conditions at the breeding locations during stopover, adjust arrival date into Iceland to when those are favorable, and avoid the risk of stochastic inclement weather prior to breeding (Newton, 2006). In fact, temperature at departure from the stopover locations tends to be positively correlated to the temperature in the breeding areas at that time (Spearman $r = 0.575$, $S = 7830$, $p < 0.001$, $n = 48$) and with the temperature upon arrival (Spearman $r = 475$, $S = 9672$, $p < 0.001$, $n = 48$), suggesting that if whimbrels depart when weather is good at the stopover site, they are likely to find favorable conditions upon arrival in Iceland. Similar behavior has been suggested for Icelandic black-tailed godwits *L. limosa islandica* (Gunnarsson and Tómasson, 2011; Alves et al., 2012), that first fly to Britain and Ireland from southern wintering areas in the Iberian Peninsula, before resuming migration to Iceland. Hence, in both species, individuals move to a region where they are likely able to adjust their arrival timing into the breeding sites. Furthermore, given that most individuals stop, a stopover might also allow timing synchronization among couples and the pair bond in the breeding grounds is maintained (Handel and Gill, 2000; Gunnarsson et al., 2004).

Undertaking a stopover might bring other benefits, for example, if individuals can attain a higher resource intake rate at the stopover than at the breeding sites (Alerstam, 2006) and arrive in better body condition (with higher energy reserves) than those that flew directly. Despite later arrival, individuals that make a stopover might then save time at the breeding sites by starting energy-demanding activities quickly (e.g., display flights; Davidson and Evans, 1988; Gudmundsson et al., 1991). On the other hand, a direct migration and early arrival might be beneficial, by guaranteeing that the partner will be met and the pair bond maintained (Ens et al., 1996). However, the relatively lower body condition of direct flight migrants might prevent earlier laying.

At the individual level, for the three birds that changed migratory behavior, the variation in all variables between direct and stopover migrations reflects the patterns also observed at the population level (i.e., tracked individuals). For example, in years when individuals performed a direct flight, departure tended to be later than when a stopover was undertaken (**Figure 2**). However, the variation within strategy is smaller, as would be expected because Icelandic whimbrels tend to be consistent in their timing, particularly at spring departure (Carneiro et al., 2019b). Given the consistency in spring departure date, the differences between direct and stopover migratory behavior at the individual level, further support the role of departure date in the migratory behavior displayed. Additionally, the fact that individuals only changed from a direct to a stopover migration, hints toward an individual refinement of behavior (**Supplementary Figure S3**). Since there appears to be no clear advantage from a direct migration, a shorter flight to a stopover site might involve fewer risks due to unpredictable weather conditions at arrival and fuel depletion, while still allowing a timely arrival at the breeding sites.

Our analyses suggest that weather conditions encountered during migration are not the main driver of different spring migratory behavior in Icelandic whimbrels, but these results need to be considered with caution and may require further investigation. First, due to the naturally low prevalence of direct spring migrations, the sample size is skewed toward stopover, which may lead to type II errors, despite the good fit of our models to the data, as assessed by Hosmer & Lemeshow goodness of fit test. Second, in our main statistical models, individual identity was not included as a random effect (see section Materials and Methods), but a reduced model of migratory behavior in function of departure date suggests that individual identity may explain some of the variation in behavior, although the reduced size likely limits detection of the main effect. Nevertheless, despite being highly consistent (Carneiro et al., 2019b), individuals can perform both behaviors and vary in departure time in the same way as the population, e.g., by showing a later departure during direct migrations (**Figure 2**). Third, given that whimbrels tend to depart in flocks from the wintering sites (Piersma et al., 1990), individual decision may be influenced by group decision. However, there is evidence of flocks breaking at departure (Piersma et al., 1990), suggesting dissimilarity in group and individual behavior. In our dataset, only in four occasions whimbrels may have departed on the same flock (four times two individuals), and in two of those they clearly took different flight routes either due to departing in different flocks, or to the flock breaking up following departure (**Supplementary Figure S4**). Hence, the effects of weather and departure date are unlikely to be biased by non-independence between tracked individuals. Fourth, there is error associated with locations extracted from geolocators (Phillips et al., 2004; Shaffer et al., 2005; Fudickar et al., 2012), and also on the interpolated weather variables (Kemp et al., 2012a), which may influence the direction and speed calculated, and consequently influencing FA and AGR. However, given the amount of locations during migration available in our dataset, if wind conditions had an important effect, it should still be detected. Fifth, we used FA as the tailwind component, which is a method with few assumptions that ignores perpendicular wind flow in relation to the direction of the birds movement (Kemp et al., 2012b), therefore simplifying a likely more complex behavior. Lastly, as the flight altitude of the individuals tracked here is unknown, we assumed whimbrels fly at constant altitude which restricts the natural dynamics of flight.

Several studies have investigated the role of weather conditions on the decision to depart from stopover locations (e.g., Schaub et al., 2004; Grönroos et al., 2012; Schmaljohann et al., 2013; Packmor et al., 2020), but less has been done concerning their role in the decision to stop during migratory flight (Beekman et al., 2002; Anderson et al., 2019). We add knowledge on the latter, by showing that weather conditions experienced during flight appear to be irrelevant for Icelandic whimbrels, as individuals seem to define a strategy prior to or at departure from the wintering sites. Whether departure date is a cause or a consequence of a direct or stopover spring migration remains to be investigated, but records of whimbrels' body condition prior to departure from the wintering grounds will likely help to clarify this question.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The studies involving whimbrels were reviewed and approved by the Bird Ringing Unit of the Icelandic Institute of Natural History according to Act no. 64/1994.

AUTHOR CONTRIBUTIONS

CC performed the analysis and led the writing with substantial discussion and inputs from TG and JA. All authors designed and carried the study, read and approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00145/full#supplementary-material

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Compensatory Breeding in Years Following Drought in a Desert-Dwelling Cooperative Breeder

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Variation in weather patterns can influence reproductive effort and success not only within but also between breeding seasons. Where environmental conditions can be highly variable between years, the weather, and particularly extreme weather events such as heat waves and droughts, may exert a strong influence on reproductive effort (number of breeding attempts) and success (number of surviving young) from one breeding season to the next. We used a 15-year dataset for a cooperatively breeding bird, the southern pied babbler *Turdoides bicolor*, to determine the impact of high temperatures and drought on reproductive effort and success. We tested the influence on reproductive effort and success of mean daily maximum air temperature and drought both within a breeding season, to determine the relative importance of current conditions, and during the previous breeding season, to determine the relative importance of compensatory effects in response to prior conditions. Reproductive effort and success were lower during breeding seasons characterized by drought, and higher in the breeding seasons that followed droughts, but were not predicted by mean daily maximum temperatures measured over the full length of the breeding season. We provide evidence of compensatory breeding following drought in a bird species endemic to a semi-arid ecosystem and suggest that compensatory mechanisms may be an important part of both long-term population persistence and post-drought population recovery.

Keywords: climate change, compensatory breeding, cooperative breeding, drought, environmental change, southern pied babbler, weather

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INTRODUCTION

The sequential, and often cyclical (Korpimäki, 1986; Marra et al., 2015; Nater et al., 2018), nature of biological systems means that each event or process experienced by an individual may have measurable downstream effects (Harrison et al., 2011). Non-fatal effects, such as poor physical condition or delayed breeding, can influence reproduction or survival over time (Marra et al., 2015). Variations in seasonal weather patterns and the occurrence of extreme weather events such as droughts, floods, and heatwaves are among the primary drivers of variation in individual success in vertebrates, influencing reproduction and survival both directly and indirectly, often via effects on resource availability (Harrison et al., 2011). To date, most research on the within and between season effects of weather patterns and extreme events has focused on the influence *within* an annual cycle (Saino et al., 2011; Laplante et al., 2019) of (a) conditions during early development on individual success as a nestling (Pérez et al., 2008; Auer and Martin, 2017; Ospina et al., 2018), fledgling (Blomberg et al., 2014; de Zwaan et al., 2019), or adult (Porcelli et al., 2016; Hsu et al., 2017; Marshall et al., 2017) and (b) seasonal weather conditions on body mass (Loison and Langvatn, 1998; van de Pol et al., 2016), behavior (Akresh et al., 2019; Rauber et al., 2019), survival (Berryman and Lima, 2006; Gardner et al., 2017, 2018; Woodworth et al., 2017; Chiffard et al., 2019), and reproductive investment (Clutton-Brock et al., 1991; Monteuil-Spencer, 2017).

Effects of extreme weather events can be cumulative, and can have devastating consequences for population persistence (Cruz-McDonnell and Wolf, 2016; Wingfield et al., 2017; Bourne et al., 2020b), particularly if such events re-occur more quickly than populations are able to recover from them (Enright et al., 2015). Although weather conditions in highly seasonal temperate environments can vary considerably between years (Griesser et al., 2017), distinct seasonal weather patterns lead to the relatively predictable onset and duration of annual breeding seasons (Greño et al., 2008; Simmonds et al., 2017; Laplante et al., 2019). This differs somewhat from more arid sub-tropical environments, where breeding seasons typically span many months and animals respond flexibly and opportunistically to highly variable weather conditions and less defined seasonality (Griffith et al., 2016; Hidalgo Aranzamendi et al., 2019). In hotter, drier, and less predictable environments, the effects of variation in weather patterns and of extreme weather events may manifest as foregone or failed breeding in poor years (McCreedy and van Riper, 2015; Conrey et al., 2016; van de Ven, 2017; Cooper et al., 2019; Moore and Martin, 2019; Sharpe et al., 2019). This may subsequently lead to greater investment in breeding in relatively more favorable years (Jetz and Rubenstein, 2011; Lerch et al., 2018), but this effect has received much less research attention.

Few studies have explicitly tested the different explanatory power of processes occurring within vs. between annual cycles to predict survival and reproductive success [although see Gardner et al. (2017) and Griesser et al. (2017)]. Additionally, few studies have considered the effects of weather conditions in one breeding season on individual success in the subsequent breeding season [although see Moyes et al. (2006)]. Species living in more arid sub-tropical environments are potentially useful models for studying the effects of weather patterns and extreme events between years, because these ecosystems are characterized by high interannual variability and frequent extremes in temperature and rainfall (McKechnie et al., 2012). High temperatures and droughts have been linked to delayed or failed reproduction in a number of arid and semiarid-zone species (Cunningham et al., 2013; Cruz-McDonnell and Wolf, 2016; Nater et al., 2018; van de Ven et al., 2020a). Compensatory responses to severe weather events, like heat waves and droughts, may act over relatively long timescales to reduce or offset the negative effects of exposure to high temperatures or drought on reproductive success. These could be extremely important for population persistence over time (Wiley, 2017; Paniw et al., 2019), yet have been relatively little studied in subtropical environments.

Here, we consider the relative influence of weather conditions within vs. between annual cycles (consecutive austral summer breeding seasons) on reproductive effort (number of clutches laid and incubated) and success (number of young surviving to nutritional independence) in a cooperatively breeding bird, the southern pied babbler *Turdoides bicolor* (hereafter "pied babblers"), endemic to a semi-arid subtropical region in southern Africa. We explore the potential for compensatory mechanisms in response to severe weather conditions characteristic of semi-arid environments, specifically high temperatures and drought. We additionally consider the influence of group size on reproductive effort and success, and whether effects of high temperatures or drought were moderated by group size. Cooperative species may respond differently to external stressors than non-cooperative species, because reproductive outcomes can be affected by both the presence and behavior of other group members (Crick, 1992; Cockburn et al., 2008; Meade et al., 2010; Langmore et al., 2016; Wiley and Ridley, 2016). We predict that high temperatures and drought experienced within a breeding season will suppress both reproductive effort and success, and that pied babblers will compensate for this suppression by increasing investment in reproductive effort and success in breeding seasons that follow hot and dry conditions. We expect positive effects of group size on both reproductive effort and success, hypothesizing that, if cooperation helps to buffer against environmental effects (Rubenstein and Lovette, 2007; Cornwallis et al., 2017; Lukas and Clutton-Brock, 2017; van de Ven et al., 2020a), reproduction should be less affected by high temperatures and drought in larger groups.

METHOD

Study Site and System

Fieldwork was undertaken at the 33 km^2 Kuruman River Reserve (KRR; 26°58'S, 21°49'E) and neighboring farms in the southern African Kalahari. Droughts are a regular feature of the local climate (Jury, 2013; Tokura et al., 2018) and rainfall has been declining, and high temperature extremes increasing in both frequency and severity, over the last 20 years (Kruger and Sekele, 2013; van Wilgen et al., 2016; van de Ven, 2017).

Pied babblers are medium-sized (60–90 g), cooperatively breeding passerines (Ridley, 2016). Groups range in size from 3 to 15 individuals, consisting of a single breeding pair with subordinate adult helpers (Nelson-Flower et al., 2011). Pied babblers are sexually mature one year after hatching and are defined as adults at this age (Ridley, 2016). Pied babblers may attempt to breed several times within a single breeding season, re-laying if breeding attempts fail and/or if conditions allow (Ridley and Raihani, 2008; Raihani et al., 2010). They can also produce overlapping broods, whereby the breeding pair initiates and incubates a new clutch while the helpers are still feeding dependent fledglings from a previous breeding attempt (Ridley and Raihani, 2008). Some breeding occurs over winter when there has been late-season rain, but the breeding season typically extends from September to March (austral summer) (Ridley, 2016; Bourne et al., 2020a) and thus annual breeding cycles cross calendar years.

Groups in the study population were visited weekly during each of the 15 breeding seasons between September 2005 and February 2020 to check group composition and record life history events such as breeding, immigration, and dispersal. Pied babblers are territorial and groups can be reliably located by visits to each territory (Golabek et al., 2012). Detailed life-history data have been collected from a study population of pied babblers at the KRR since 2003 (Ridley and Raihani, 2007; Ridley, 2016). Birds in the study population are habituated to observation at distances of 1–5 m and uniquely identifiable by a combination of metal and color leg-rings (Ridley and Raihani, 2007).

Data Collection

Breeding Effort and Success

Breeding effort was defined as the number of breeding attempts initiated, as determined by the number of discrete clutches laid and incubated per group per breeding season. Breeding success was defined as the total number of nutritionally independent young raised per group per season. Fledglings are considered nutritionally independent by 90 days of age (calculated from day of hatching), by which age they typically receive <1 feed per hour from adult group members (Ridley and Raihani, 2007).

Collection of nest life history data followed Ridley and van den Heuvel (2012): nests were located by observing nest-building during weekly monitoring visits; incubation start, hatch, and fledge dates were determined by checking nests every two to three days; and breeding attempts were considered to have failed when nests were no longer attended or dependent fledglings were not seen on two consecutive visits. In most cases, it was not possible to determine the proximate cause of nest failure or fledgling death. Average group size (the average number of adults present in the group over a breeding season; mean = 4.1 ± 1.4, range: 2–9) was recorded for each group per breeding season.

Temperature and Rainfall

Daily maximum air temperature (T_{max}, °C) and rainfall (mm) data were collected from an on-site weather station (Vantage Pro2, Davis Instruments, Hayward, United States). Missing data from 2009, 2010, and 2011 were sourced from a nearby South African Weather Services weather station (Van Zylsrus, 28 km from the KRR) which produces significantly repeatable temperature measurements (Lin's concordance correlation coefficient $r_c = 0.957$, 95 % CI: 0.951–0.962), and moderately repeatable rainfall measurements ($r_c = 0.517$, 95 % CI: 0.465–0.566) in comparison with the on-site weather station. Differences in rainfall were small (mean difference = 0.045 ± 3.075 mm; 95 % CI = -5.981 to 6.072 mm), suggesting that both weather stations adequately detected wet vs. dry periods. Long term rainfall data for the region, used to determine the presence or absence of a meteorological drought within a breeding season, was obtained from a South African Weather Services weather station at Twee Rivieren (∼120 km from the KRR; available until 2013).

Daily T_{max} values were averaged for each breeding season in which nest monitoring occurred (September–March, $\mathrm{MeanT}_{\mathrm{MaxSeason}(1,2,..,t)}$), and for the preceding breeding season (previous September–March, $\mathrm{Mean\ T}_{\mathrm{MaxSeason}(t-1)}$). Rainfall was summed for each breeding season in which nest monitoring occurred ($\mathrm{Rain}_{\mathrm{Season}(t)}$), and for the preceding breeding season ($\mathrm{Rain}_{\mathrm{Season}(t-1)}$). Following Mayaud et al. (2017), meteorological drought within a breeding season ($\mathrm{Drought}_{\mathrm{Season}(t)}$) or preceding breeding season ($\mathrm{Drought}_{\mathrm{Season}(t-1)}$) was defined as ≤75% of average precipitation between September and March (≤135.75 mm), using the 30-year period 1984–2013 to determine average precipitation.

Statistical Analyses

Statistical analyses were conducted in R v 3.4.1 R Core Team (2017). To determine which variables predicted (a) number of breeding attempts and (b) breeding success per group per year, we used generalized linear mixed effects models with a Poisson distribution (log link) in the package *lme4* (Bates et al., 2015). Model selection with Akaike's information criterion corrected for small sample size (AICc) and maximum likelihood estimation was used to test a series of models to determine which best explained patterns of variation in the data (Harrison et al., 2018). Where multiple models were within 5 AICc of the top model, top model sets were averaged using the package *MuMIn* (Barton, 2015). All continuous explanatory variables were scaled by centering and standardising by the mean (Harrison et al., 2018). Rainfall and drought within the same annual cycle were highly correlated ($F_{1,154} \geq 359.940$, $p < 0.001$), since these variables represent the same pattern in different ways. We used the categorical variable, drought vs no drought, as the rainfall parameter in all analyses because models including this variable had a consistently lower AICc. Drought is also of direct interest for our study because it represents the presence or absence of extreme weather in our study system. Measures of temperature and drought were also correlated ($F_{1,154} \geq 9.706$, $p < 0.002$), with droughts typically occurring in hotter years. Group sizes were slightly smaller in years following droughts, but the difference is not statistically significant (mean group size in breeding seasons following drought = 4.1 ± 1.3; mean group size in breeding seasons following no drought = 4.6 ± 1.5; $F_{1,188} = 2.515$, $p = 0.116$). Correlated variables were not included in the same additive models, but interactions between correlated variables were tested (Harrison et al., 2018). Model terms with confidence intervals not intersecting zero were considered to explain significant patterns within our data (Grueber et al., 2011). Model fits were assessed by checking dispersion parameters using the package *RVAideMemoire* (Herve, 2019).

Groups in which the breeding pair split during the breeding season (n = 18 of 177 group-seasons) were excluded from analysis, since the continuity of the breeding pair is an important determinant of reproductive success in pied babblers (Wiley and Ridley, 2018). Exploratory analyses showed that reproductive allocation in the previous season (e.g., number of days invested in breeding in $\text{Season}_{(t-1)}$) were not associated with variation in breeding effort or success in our study system, and we therefore did not include prior reproductive allocation in the model sets tested here (see **Supplementary Tables S1–S4** and **Supplementary Figure S1**). Average group size, $\text{Drought}_{\text{Season}(t)}$, $\text{Drought}_{\text{Season}(t-1)}$, $\text{MeanT}_{\text{MaxSeason}(t)}$ and $\text{MeanT}_{\text{MaxSeason}(t-1)}$, and the two-way interactions between all climate and group size variables were included as fixed effects, with group identity included as a random effect in both analyses. Since interactions between group size and environmental parameters on reproduction could provide evidence for a moderating effect of group size, we conducted sensitivity power analyses (Cohen, 1988; Leon and Heo, 2009; Greenland et al., 2016), using the package *pwr* (Champely et al., 2018), to confirm that we had sufficient sample size to detect small main effects in both analyses (Cohen's $f^2 < 0.06$) and moderate-large effects of two-way interactions in analyses of reproductive effort ($f^2 = 0.17$) and reproductive success ($f^2 = 0.27$).

RESULTS

The average summer maximum daily temperature at the study site from 2005 to 2020 was 34.5 ± 1.4°C (range in annual average summer maximum temperatures, September–March, 32.4–37.8°C). Summer rainfall averaged 174.0 ± 70.1 mm (range 64.4–291.2 mm). Droughts occurred in 6 of 15 summer breeding seasons studied (2006/07, 2012/13, 2014/15, 2015/16, 2018/19, and 2019/2020; **Figure 1**). $\text{Drought}_{\text{Season}(t)}$ and $\text{Drought}_{\text{Season}(t-1)}$ were independent ($X^2{}_1 = 0.228$, $p = 0.633$). Group size averaged 4.1 ± 1.4 adults per group per season (range 2–9 adults), and we analyzed data from an average of 13 ± 4 groups per breeding season (range 6–19 groups).

We observed particularly large increases in the total number of breeding attempts in several breeding seasons that followed a drought ($\text{Drought}_{\text{Season}(t-1)}$; for example, see 2013/2014 and 2016/2017 in **Figure 1**).These increases were disproportionate to the amount of precipitation recorded within the breeding season ($\text{Rain}_{\text{Season}(t)}$). The number of breeding attempts per group varied between breeding seasons (range 1–9, mean = 3.2 ± 1.8; n = 190 group-seasons). Breeding effort was lower in breeding seasons characterized by drought ($\text{Drought}_{\text{Season}(t)}$), averaging 2.1 ± 0.9 attempts per group compared to 4.0 ± 1.9 attempts in non-drought breeding seasons (**Figure 2** and **Table 1**). Breeding effort increased when there had been a drought in the previous breeding season ($\text{Drought}_{\text{Season}(t-1)}$), averaging 4.1 ± 2.2 attempts per group in breeding seasons preceded by drought compared to 2.8 ± 1.5 attempts when not preceded by drought (**Figure 2** and **Table 1**). We found no evidence for an effect of temperature, group size, or any interaction between group size and weather on the number of breeding attempts per group per season (see **Supplementary Table S5** for full model output).

Breeding success per group varied between breeding seasons (range 0–7 independent young produced, mean = 1.6 ± 1.5; n = 156 group-seasons) and, like the number of breeding attempts, was suppressed in breeding seasons characterized by drought within the current breeding season ($\text{Drought}_{\text{Season}(t)}$), averaging 1.0 ± 1.1 surviving young per group compared to 1.9 ± 1.7 surviving young in non-drought breeding seasons (**Figure 3** and **Table 1**). Breeding success increased when there had been a drought in the previous breeding season ($\text{Drought}_{\text{Season}(t-1)}$), averaging 2.1 ± 1.7 surviving young per group in breeding seasons preceded by drought compared to 1.4 ± 1.4 attempts when not preceded by drought. Larger

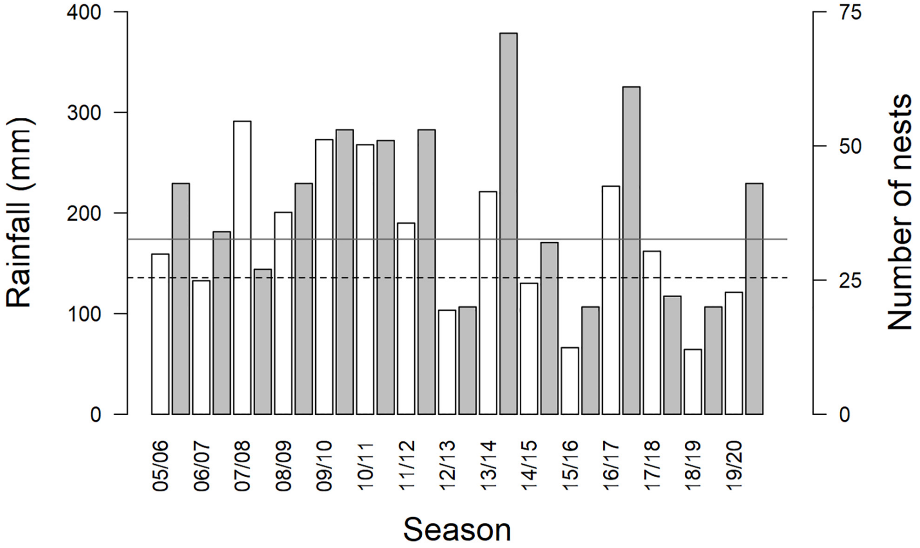

FIGURE 1 | Total rainfall (mm, white bars) and number of nests (gray bars) per austral summer breeding season (September–March). Drought occurred in six of fifteen breeding seasons. Rainfall bars below the dashed line at 135.75 mm rainfall indicate drought. Mean rainfall for the study site (174 mm) is shown on the figure by the gray solid horizontal line. Increases in the number of nests disproportionate to increases in rainfall occurred in several years following drought (e.g. 13/14, 16/17).

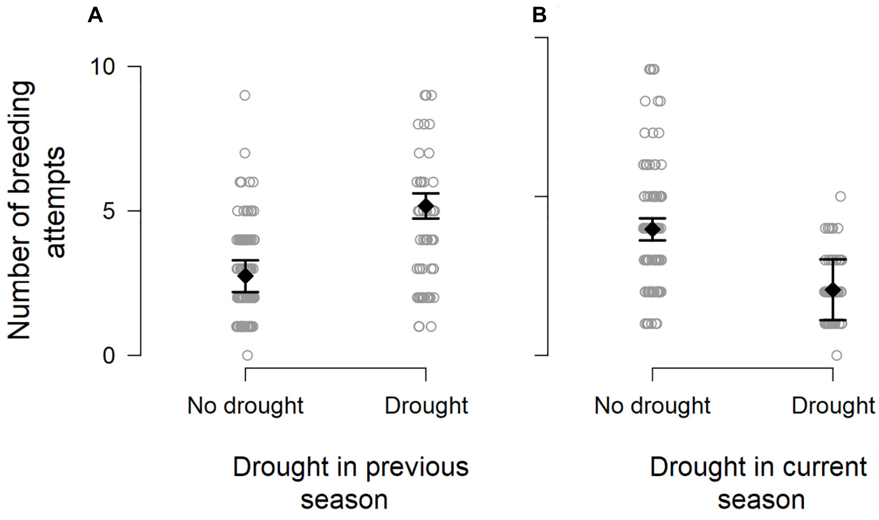

FIGURE 2 | Number of breeding attempts initiated per group per breeding season in relation to **(A)** the occurrence of drought in a previous breeding season, showing the model-predicted mean (black filled diamond) ± 1.96 × standard error (black whiskers), and **(B)** the occurrence of drought during the current breeding season. Data points are jittered for improved visibility.

TABLE 1 | Top GLMM model sets for analyses on the number of breeding attempts per group per season (*n* = 190 group-seasons from 39 groups over 15 breeding seasons) and the number of surviving young per group (*n* = 156 group-seasons from 32 groups over 15 breeding seasons).

	AICc	*ΔAICc*	*ωi*
Response: number of breeding attempts			
Null model	746.40	68.95	0.00
Top model set			
Drought$_{\text{Season(t)}}$ + Drought$_{\text{Season(t−1)}}$	675.60	0.00	1.00
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	1.241	0.058	1.125/1.354
Drought$_{\text{Season(t−1)}}$ (drought = 1)	**0.363**	**0.083**	**0.200/0.524**
Drought$_{\text{Season(t)}}$ (drought = 1)	**−0.635**	**0.093**	**−0.819/−0.456**
***Residual deviance: 115.708 on 186 degrees of freedom (ratio: 0.622)**			
Response: number of surviving young			
Null model	535.90	28.89	0.00
Top model set			
Average group size + Drought$_{\text{Season(t)}}$ + Drought$_{\text{Season(t−1)}}$ + Mean T$_{\text{maxSeason(t−1)}}$	507.01	0.00	0.51
Average group size + Drought$_{\text{Season(t)}}$ + Drought$_{\text{Season(t−1)}}$	507.31	0.30	0.44
Average group size + Drought$_{\text{Season(t)}}$ + Mean T$_{\text{maxSeason(t−1)}}$	511.77	4.76	0.05
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	0.401	0.115	0.175/0.627
Average group size	**0.207**	**0.068**	**0.072/0.343**
Drought$_{\text{Season(t−1)}}$ (drought = 1)	**0.403**	**0.170**	**0.067/0.739**
Drought$_{\text{Season(t)}}$ (drought = 1)	**−0.514**	**0.166**	**−0.841/−0.187**
Mean T$_{\text{maxSeason(t−1)}}$	0.072	0.086	−0.099/0.242
***Residual deviance: 198.982 on 151 degrees of freedom (ratio: 1.318)**			

Model averaging was implemented on all models with ΔAICc <5. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets. The reference level for Drought variables is 0 (no drought). See ***Supplementary Material*** *for full model outputs.*

groups produced more surviving young than smaller groups (**Figure 3C** and **Table 1**), but there was no evidence for an effect of temperature or any interaction between group size and weather on breeding success (see **Supplementary Table S6** for full model output).

DISCUSSION

We investigated the relative importance of impacts of within and between year variation in temperature, rainfall, and group size on reproduction in a cooperatively breeding bird, and

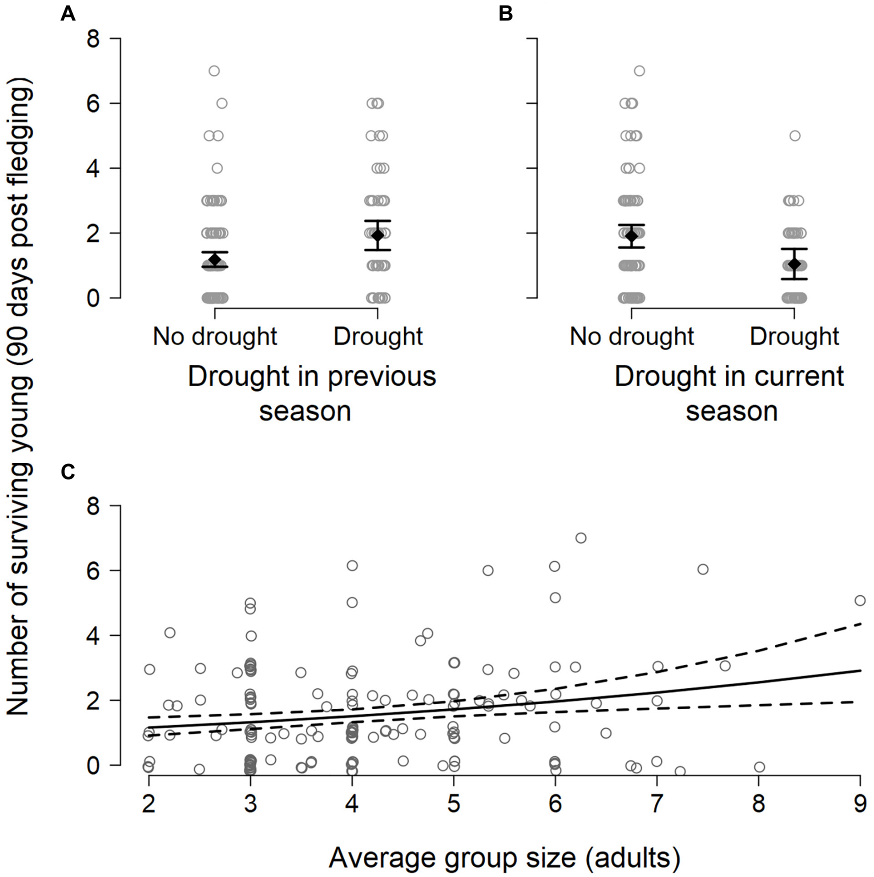

FIGURE 3 | Number of surviving young (90 days post fledging) produced per group per breeding season in relation to **(A)** the occurrence of drought in a previous breeding, showing the model-predicted mean (black filled diamond) ± 1.96 × standard error (black whiskers), **(B)** the occurrence of drought during the current breeding season, and **(C)** average group size during the current breeding season. Data are jittered for improved visibility.

the potential role of compensatory mechanisms in response to drought. Both breeding effort and success were lower in pied babblers when they experienced droughts during the breeding season. Pied babbler groups initiated more breeding attempts and were more successful in breeding seasons *following* drought, indicating the presence of compensatory behavior in response to harsh conditions. Drought was the most important climate-related predictor of reproductive effort and success in pied babblers, a finding which is consistent with other studies of birds breeding in subtropical environments (Morrison and Bolger, 2002; Skagen and Yackel Adams, 2012; Zuckerberg et al., 2018; Hidalgo Aranzamendi et al., 2019). While high temperatures during breeding attempts are commonly associated with reduced reproductive success in birds (Cunningham et al., 2013; van de Ven et al., 2020b), including in this population of pied babblers (Wiley and Ridley, 2016; Bourne et al., 2020a), we did not find strong effects of mean daily maximum temperatures calculated over the full length of the breeding season. Our broad-scale analysis considers all breeding attempts within a season, rather than individual nests or fledglings, and, in semi-arid systems, temperature effects are often immediate and direct [via effects on physiology of individuals (McKechnie, 2019)], while rainfall effects are often lagged and generally indirect [via effects on available food resources (Cumming and Bernard, 1997; Hidalgo Aranzamendi et al., 2019)]. Our decision to analyze the data at the scale of the full breeding season may, therefore, explain why we identify stronger drought than temperature effects. We found no evidence that group size interacted with climatic factors to moderate the effects of climate extremes: while larger groups were able to produce more surviving young than smaller groups on average (also see Ridley, 2016; Ridley and van den Heuvel, 2012), this pattern did not vary according to climatic conditions.

Pied babblers undertake most breeding during September to December each year, largely independent of rainfall (Bourne et al., 2020a), but will breed until later in the season in response to rainfall within the breeding season (Ridley, 2016). Pied babblers are able to re-clutch while raising dependent fledglings when conditions allow, due to the presence of task partitioning among group members (Ridley and Raihani, 2008; Ridley and van den Heuvel, 2012). These reproductive behaviors provide a mechanism through which pied babblers can respond flexibly to interannual variation in rainfall, laying and incubating more clutches and producing more surviving young in breeding seasons that follow a drought. An alternative explanation for the pattern that we observed could be that higher numbers of clutches initiated in non-drought years indicate higher rates of nest predation, an important cause of reproductive failure in birds (Mayer et al., 2009; DeGregorio et al., 2015; Mortensen and Reed, 2018). Previous research in sociable weavers (*Philetairus socius*) has shown that reproductive effort (defined as number of clutches laid and incubated) increases when predation is high (Mares et al., 2017). In cases of high reproductive effort in response to high predation risk, the number of fledglings produced per breeding attempt is typically low (Mares et al., 2017). Additionally, in arid environments, higher predation rates are often associated with warm, dry weather (McCreedy and van Riper, 2015; Kozma et al., 2017). Our results show that pied babblers produced fewer surviving young during droughts and more surviving young per breeding attempt in breeding seasons following a drought. This represents an effect of greater investment in breeding during breeding seasons following a drought, rather than simply more clutches being laid due to higher rates of predation or nest failure. The pattern of producing more surviving young per breeding attempt in breeding seasons following a drought also cannot be explained by years following droughts being significantly wetter (Iknayan and Beissinger, 2018; Sharpe et al., 2019), since droughts were not consistently followed by wetter conditions (**Figure 1**).

We found that larger groups of pied babblers produced more surviving young, a benefit of cooperation that may be important for post-drought recovery and overall population persistence in this species (Wiley, 2017). The observed group size effect is likely driven by the presence of helpers reducing predation risk at nests (Raihani and Ridley, 2007; Valencia et al., 2016), and enabling the production of multiple, overlapping broods per breeding season (Ridley and Raihani, 2008; Valencia et al., 2016). Cooperative species also tend to raise more broods to independence per breeding season than non-cooperative species (Ridley and van den Heuvel, 2012). Group size did not interact with temperature or rainfall to predict either reproductive effort or reproductive success, suggesting that breeding pied babblers respond similarly to variation in the weather regardless of helper number (van de Ven et al., 2020a). Flexible responses to drought, including compensatory breeding in breeding seasons following a drought, were observed across all group sizes, confirming that pied babblers do not vary their response to climatic conditions in relation to group size.

In summary, we demonstrate that weather conditions in both previous and current annual cycles exert a powerful influence on reproductive effort and success in a cooperatively breeding, desert-adapted passerine. Cooper et al. (2019) and Griesser et al. (2017) provide evidence that birds across a range of environments can distinguish relative weather conditions over shorter timescales and may be able to adjust their reproductive allocation depending on variable within-season weather conditions. Our data suggest that pied babblers can respond to relative conditions over fairly long timescales and, importantly, they may engage in compensatory breeding when environmental conditions allow (see Hatchwell, 1999 for compensatory adjustments to parental care in cooperatively breeding birds). Compensatory breeding in years following drought is therefore likely to be an extremely important part of post-drought recovery and overall population persistence in this (Wiley, 2017) and other species (van de Ven, 2017; Paniw et al., 2019). However, given that rapid increases in the frequency and severity of droughts are predicted under climate change (MacKellar et al., 2014; Wise and Lensing, 2019), compensatory mechanisms which have been successful at maintaining populations in the past may prove insufficient to allow population recovery between extreme events (Enright et al., 2015; Cruz-McDonnell and Wolf, 2016). An improved understanding of the ways in which animals employ flexible breeding strategies and compensatory mechanisms is thus critical for informing population viability models and conservation management actions when accounting for the impact of climate variability and change on animal populations.

DATA AVAILABILITY STATEMENT

The datasets underlying all analyses presented in this study have been archived at the University of Cape Town's open access institutional data repository, ZivaHub (a figshare platform), where they are publicly available at doi: 10.25375/uct.12471569.v1.

ETHICS STATEMENT

Permission to conduct this research was given by the University of Cape Town Animal Ethics Committee under animal ethics permit numbers R2012/2006/V15/AR and 2016/V6/SC and by the South African Department of Environment and Nature Conservation under fauna research permit number 1216/2016.

AUTHOR CONTRIBUTIONS

AR started habituation of the study animals and collection of life history data in 2003 and has maintained it ever since; this was central to making the study possible. AB undertook all fieldwork from 2016 onwards and drafted the manuscript. AB and AR analyzed the data. All authors conceived the study, contributed substantially to revisions, and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00190/full#supplementary-material

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High Rates of Exposure to Simulated Winter Storm Cues Negatively Affect White-Throated Sparrow (*Zonotrichia albicollis*) Energy Reserves

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Birds are often able to cope with, and respond to, inclement weather with physiological and behavioral responses. As storms become more severe or frequent as a result of climate change, the adaptive coping responses of many species may be pushed beyond current tolerance limits. We investigated the effects of experimental recurrent inclement winter weather cues on body composition, glucocorticoid hormones, and behavior of white-throated sparrows (*Zonotrichia albicollis*). We used a hypobaric climatic wind tunnel to simulate storms by transiently decreasing barometric pressure and temperature, and measured behavioral responses, body composition, and baseline corticosterone levels in birds exposed, or not exposed (control), to different frequencies of simulated storms. In study 1, experimental birds were exposed to one storm per week over 9 weeks. In study 2, experimental birds were exposed to two storms per week over 12 weeks. Birds exposed to one simulated storm per week had higher fat and lean masses than control birds, with no differences in the amount of time groups spent feeding. This change in body composition suggests that birds were coping by increasing energy stores. In contrast, birds exposed to two simulated storms per week had lower fat masses compared to control birds, even though they spent more time feeding. Experimental birds in study 2 also had lower baseline corticosterone levels than controls. These changes suggest that the coping response observed in study 1 was not possible in study 2. These findings provide novel experimental evidence that birds detect and respond to changes in temperature and barometric pressure independent of other storm-related cues. One simulated storm per week resulted in potentially adaptive responses of increased mass. However, increasing the frequency of storm exposure to twice per week exceeded the birds' capacity to maintain these energy reserves. These results also experimentally demonstrate that repeated exposure to inclement weather cues can directly affect birds' energy reserves, even in the absence of a storm itself, with strong implications for survival as severe weather events continue to become more prevalent.

Keywords: storms, weather, corticosterone, stress response, songbirds

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INTRODUCTION

Birds are exposed to seasonal and daily fluctuations in environmental conditions. Predictable fluctuations are typically accommodated through biological rhythms in physiology and behavior. However, less predictable fluctuations such as rapid decline in resource availability, disease exposure, predator interactions and inclement weather can vary across temporal and spatial scales, requiring coping responses with the potential of entering an emergency life history stage (Wingfield et al., 1998). Weather conditions, specifically, can be a major factor affecting individual survival and reproductive success, both directly and indirectly (Newton, 1998). Many of the environmental factors associated with storms can pose challenges with respect to foraging behavior (Boyle et al., 2010; Breuner et al., 2013), migration (Newton, 2007; James and Abbott, 2014), territorial defense (Breuner and Hahn, 2003) and mate acquisition (Wingfield, 1985; Vitousek and Romero, 2013). Inclement weather and storms can create life threatening conditions that may continue to negatively impact individuals after the storm passes.

Although there are no universally accepted definitions of stress, many define a stressor, in part, as an unpredictable challenge (Romero, 2012). However, unpredictability alone may not induce a stress response if it does not pose a threat to an organism. For example, if an unpredictable severe weather event occurs, it may not be perceived as a stressor to birds if they have maintained energy reserves and there are ample food resources. Alternatively, a storm may be perceived as a stressor if food availability and energy reserves are low. This may result in the animal entering an emergency life-history stage since the current metabolic demands of the birds cannot be met (Wingfield et al., 1998). When birds encounter a stressor and the emergency life-history stage is induced, physiological and behavioral responses are activated, including corticosterone secretion, reallocation of energy towards self-maintenance, and increased feeding behavior (Wingfield et al., 1998; Reneerkens et al., 2002). Factors including food availability and storm severity can thus influence whether a storm will be perceived as a stressor. Additionally, the frequency of unpredictable inclement weather may influence this response. Frequent acute stressors can cumulatively create a condition of chronic stress (Busch et al., 2008). Thus, repeated storms may act cumulatively as a chronic stressor and induce longer-term endocrine responses. Though corticosterone levels typically rise rapidly in response to an acute stressor, chronic stress may induce increased or decreased baseline corticosterone levels (Dickens and Romero, 2013).

Birds' responses to environmental perturbations can be deployed over shorter time scales to cope with inclement weather, or over longer time scales to cope with prolonged winter conditions (Carey and Dawson, 1999). These coping responses include increasing foraging activity (Metcalfe et al., 2013), facultative migrations (Boyle et al., 2010), temporarily abandoning territories (Streby et al., 2015) or nests (Thierry et al., 2013), or ceasing normal life-history stages altogether (Wingfield et al., 1998). Food availability affects how a bird will behaviorally respond, particularly during energetically demanding life-history stages or in response to energetically demanding perturbations (Carey and Dawson, 1999). Food availability can also dictate whether a bird continues with, or ceases, a life-history stage.

Rapid but transient changes in the abiotic environment, particularly in inclement weather events, are common in most terrestrial habitats. Species have evolved adaptations to cope with such events, however, climate change may be pushing some species to their tolerance limit (Freeman and Class Freeman, 2014), depending on the degree of variation in adaptive traits that currently exist in the population (Charmantier and Gienapp, 2014). As climate change advances, rapid fluctuations in abiotic factors such as temperature, precipitation, wind, and storms are increasing in severity and frequency across the globe (IPCC, 2014). It is thus important to explore both how organisms respond to individual storms, and how they cope with repeated exposure to storms.

To fully understand birds' responses to inclement weather cues, we cannot solely rely on correlational field observations. A full understanding of the responses to storms requires experimental studies where researchers can have some form of control over environmental conditions. The responses or coping mechanisms of birds to inclement weather have only recently been studied in experimental settings (Breuner et al., 2013; Metcalfe et al., 2013). Prior research has focused on how birds cope with cold winter weather (Rogers et al., 1993; Vézina et al., 2006) and their ability to predict oncoming inclement weather using cue detection of barometric pressure and temperature (Breuner et al., 2013; Metcalfe et al., 2013), but little to no research has assessed how birds respond to repeated storms over long-term periods. As well, most prior research on birds' responses to storms has focused on the breeding season and/or migration, and we have fewer data on how birds cope with storms during winter.

In this study, our objective was to determine if birds differentially respond to lower or higher rates of repeated exposure to inclement winter weather cues and whether increased exposure frequency would cause cumulative effects. Thus, we tested the hypothesis that an increased rate of exposure to inclement weather cues would elicit greater physiological and behavioral responses. We predicted that birds exposed to storm cues would exhibit changes in body composition, baseline corticosterone levels, overall movement, and feeding behavior. Birds exposed to frequent repeated winter storm cues may respond to these repeated acute stressors as chronic stressors and increase baseline corticosterone levels. We also predicted that high-frequency exposed birds should increase fat and overall body mass, as accumulating fat reserves is a main coping technique employed by wintering birds (Carey and Dawson, 1999; Kelly et al., 2002). However, if repeated storms occur more quickly than the birds' ability to deposit fat we may not see this increase in mass. Repeated exposure to simulated storm cues may not be stressful to a bird if there are excess food and energy reserves available, but if a storm occurs when food availability and energy reserves are low (i.e., birds receiving limited food access), there may be a higher perceived threat to survival and subsequent stress response, and eventually changes in baseline corticosterone levels. Thus, we also manipulated food availability (fixed diet or ad libitum) to determine if responses to storm cues are modulated by limited food availability.

MATERIALS AND METHODS

We assessed the physiological and behavioral responses of white-throated sparrows (*Zonotrichia albicollis*) to either low-frequency (once per week over nine weeks; *study 1*) or high-frequency (twice per week over 12 weeks; *study 2*) winter storm cues. These cues were simulated low-pressure systems with an associated cold front, representing inclement winter weather conditions. In the northern hemisphere, some of the most severe winter storms are associated with a low-pressure system and an accompanied cold front (Ahrens, 2012). We used a hypobaric climatic wind tunnel to experimentally control barometric pressure, temperature, and relative humidity. For each simulated storm cue exposure, we manipulated barometric pressure and temperature over approximately a 24 h period. For the first 6 h, barometric pressure and temperature would both steadily decrease until a setpoint was reached, conditions would remain constant for about 13–14 h overnight, and then increase back to housing conditions for the remainder of the 24 h. These manipulations were meant to simulate a rapid, yet realistic, storm front. Within the high-frequency experiment (study 2), half of the birds received unlimited food availability and the remaining half received limited food.

Study Species

White-throated sparrows are short-distance migrants that breed in the North American boreal forest, but still experience inclement cold winter weather conditions throughout most of their wintering range (Falls and Kopachena, 1994). Although winters in this region are becoming milder overall, there will likely be more intense and more frequent winter storms in the future (Francis and Vavrus, 2012; IPCC, 2014). Thus, the presence of inclement winter weather conditions on their wintering and breeding grounds, and their ability to adjust particularly well to captivity, make white-throated sparrows an excellent species to study the effects of inclement weather cues.

Environmental Control System; Hypobaric Climatic Wind Tunnel

We used a hypobaric climatic wind tunnel at the Advanced Facility of Avian Research, University of Western Ontario, London, Ontario, to mimic inclement weather conditions. Although the wind tunnel is normally used to study bird flight under different environmental conditions, we used the tunnel to experimentally simulate weather events (as in Metcalfe et al., 2013). The wind tunnel can control temperature between −15 and 30°C and barometric air pressure from ambient (average ∼101 kPa) down to ∼37 kPa (equivalent to ∼7000 m in altitude), and thus can be used to simulate weather-related changes in temperature and pressure (Metcalfe et al., 2013; Pellegrino et al., 2013). We housed birds in the hypobaric room (hereafter plenum) within the wind tunnel structure and did not fly birds within the tunnel section (**Figure 1**).

Study 1: Low-Frequency Exposure

For *study 1*, we caught 24 white-throated sparrows during their autumn migration in London, Ontario, Canada in October 2013. Birds were housed in individual cages (33 cm × 36 cm × 38 cm) in an environmental chamber at 11°C and provided a 50:50 mixture of ground Mazuri Small Bird Maintenance Diet (catalog number 56A6, Brentwood, MO, United States) and premium fortified budgie seed (Hagen). After being held in captivity for ∼14 weeks, birds were pseudorandomly assigned to two groups [experimental (n = 12) and control (n = 12)] counterbalanced based by wing length and plumage characteristics in an attempt to have age class and plumage morph evenly distributed between groups. All birds received the same fixed amount of 8 g of food per day. Food amounts of 8 g per day were previously verified to provide birds enough energy to maintain stable body condition. Providing a fixed diet was done so that birds had sufficient food to not be food restricted, but so that they would not perceive food availability to be unlimited.

Each experimental group was housed in a separate environmental chamber, with birds in individual cages within. All birds were held at a constant 11°C under ambient barometric pressure and kept under a winter photoperiod (∼10 h light:14 h dark) that was adjusted weekly to natural outdoor conditions. Across their wintering grounds in the eastern United States, 11°C is a realistic average temperature during the wintering months for white-throated sparrows (NOAA National Centers for Environmental Information, 2015), however, this temperature can fluctuate widely depending on storm systems passing through the region.

Study 1 Procedure

Once per week over a 9-week period beginning in January 2014, we simulated inclement winter weather cues using the hypobaric climatic wind tunnel. Experimental birds were transferred from their home environmental chamber into the wind tunnel plenum in their individual cages for a 24 h period (**Figure 1**). Once in the wind tunnel plenum, experimental birds experienced a decrease in temperature from 11 to 1°C, a decrease in barometric pressure from ambient to 96 kPa, and a consistent shift in air water content to maintain ∼60% relative humidity (**Figure 2**). Temperature decreased at an average rate of 1.9°C per hour. The average rate of decreasing air pressure varied depending on ambient pressure conditions that day. Temperature was held at 1°C for ∼14 h, following which temperature increased at ∼3°C per hour until the holding temperature of 11°C was reached. Air pressure was also increased after 14 h at an average rate of ∼1 kPa per hour until ambient pressure was reached (**Figure 2**), but this varied daily. Following this manipulation, birds were transferred back to their home environmental chambers and remained undisturbed for the remainder of the day.

Control birds were held in consistent environmental conditions throughout the duration of the experiment that matched the conditions experienced by experimental birds in their home environmental chamber (11°C, ambient barometric pressure, winter photoperiod). Control birds were also transferred to the hypobaric wind tunnel plenum once per week for a 24 h period over nine weeks, but they were held at the control

FIGURE 1 | Experimental caging in the wind tunnel plenum. Sparrows were held individually in cages on racks adjacent to the working (flight) section of the wind tunnel that can be observed to the left. A baffle (white panel) ensured air mixing between the plenum and working section so that temperature, humidity, and pressure in the plenum was identical to the air flow in the tunnel.

temperature of 11°C and under ambient barometric pressure. After 24 h, birds were brought back to their environmental chambers and left alone for the remainder of the day.

Study 2: High-Frequency Exposure

For *study 2* we caught 24 white-throated sparrows during their autumn migration in London, Ontario, Canada and near Long Point, Ontario, Canada in October 2015. All birds were brought to the Advanced Facility for Avian Research and housed in individual cages (33 cm × 36 cm × 38 cm) at 11°C under ambient barometric pressure and kept on a winter photoperiod (∼10 h light: 14 h dark) that was adjusted weekly to natural outdoor conditions. Birds were also pseudorandomly assigned to two groups [experimental (n = 12) and control (n = 12)], with half of the birds in each group receiving limited or unlimited food availability. The housing conditions, environmental conditions, and food availability was identical to conditions in *study 1*.

Study 2 Procedure

Over a 12-week period beginning in January 2016, inclement winter weather cues were simulated twice per week for 24 h within the hypobaric climatic wind tunnel, increasing both the frequency of manipulations per week and the overall duration of the study compared to *study 1*. Wind tunnel manipulations occurred over 11 weeks and the final week involved only data collection (see below; **Figure 2**). Due to an equipment failure only a single pressure manipulation occurred during the second week of this study (**Figure 2**). Identical methodologies and manipulation values were used between *study 1* and the present study, with the exception of the number of times birds entered the wind tunnel plenum per week (i.e., once vs. twice per week) and an additional food treatment, with birds in both groups receiving either limited food access (8 g per day, as in *study 1*) or unlimited food access. As in *study 1*, control birds were transferred into the wind tunnel the same number of times but were not exposed to storm cues.

Body Composition Analysis

For both *studies 1* and *2* we used Quantitative Magnetic Resonance (QMR) scans to non-invasively obtain body composition data, including fat mass and lean mass content from each bird (Guglielmo et al., 2011) every second week (fortnight). QMR scans occurred 5–6 days (study 1) or 2–3 days (study 2) after a wind tunnel exposure. Before each scan, we weighed each bird with a spring scale to measure total body mass. Once each scan was completed, birds were immediately returned to their

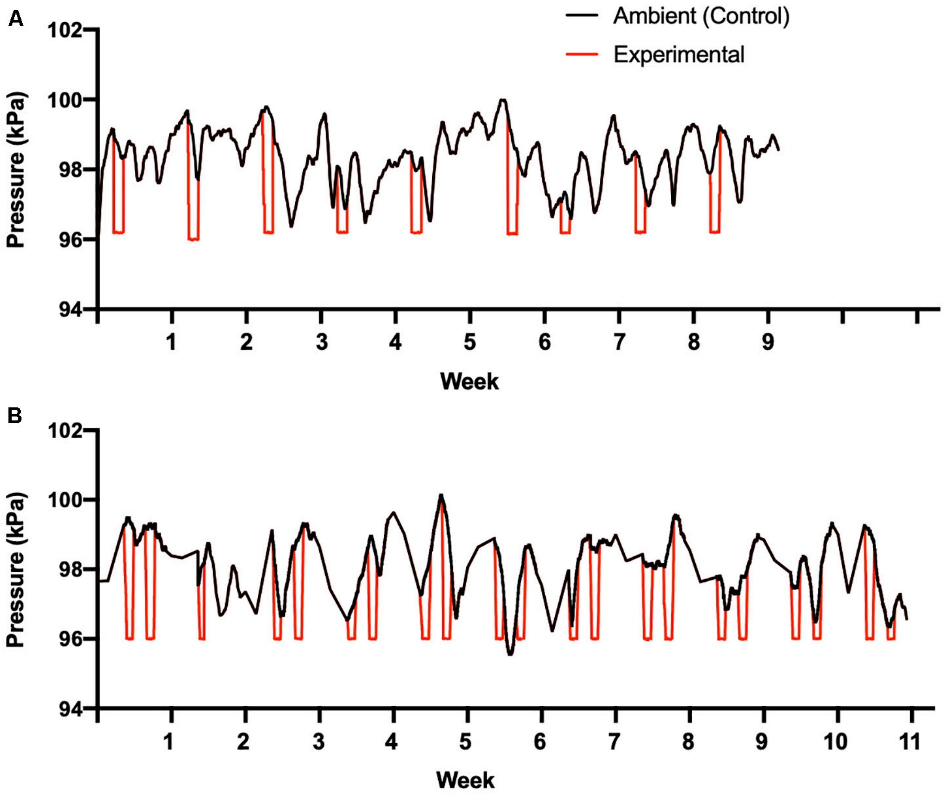

FIGURE 2 | Pressure manipulations for study 1 **(A)** and study 2 **(B)**. Black lines indicates natural changes in ambient barometric pressure during the studies, to which control birds were exposed while held at 11°C. The red lines indicates the changes in barometric pressure when experimental birds entered the wind tunnel plenum once (study 1) or twice (study 2) each week. Temperature was also decreased from 11 to 1°C for experimental birds during the times they were exposed to lowered barometric pressure.

individual cages and left them undisturbed for the remainder of the day. We scanned half the birds on either odd weeks (i.e., week 1, 3, 5, 7, 9, 11) or even weeks (i.e., week 2, 4, 6, 8, 10, 12). Since we scanned each individual bird only once every other week, the results were condensed into fortnight (2 week period), rather than analyzing the data by week.

Corticosterone Analysis

We collected blood samples from each bird every 2 weeks, on alternating weeks when birds had not been scanned with QMR. Each blood sample was collected 5–6 days (*study 1*) or 2–3 days (*study 2*) after birds had last been exposed to new housing conditions or to environmental manipulations in the wind tunnel plenum. This timing allowed birds to recover from potential acute stress experienced from being moved in and out of the wind tunnel that may influence baseline glucocorticoid levels.

All blood samples were obtained within 3 min of entering the birds' environmental chamber. Approximately 75 μL of blood was taken from the alar vein using a 26-gauge needle and collected in heparinized microhematocrit tubes. Samples were immediately placed on ice and centrifuged within 30 min of collection. Plasma was separated from red blood cells by a microhematocrit centrifuge at 13,000 g for 11 min. Plasma was stored at −30℃ until assays were run. Corticosterone levels were quantified using an enzymeimmunoassay (EIA) kit that has been previously validated in sparrows (Wada et al., 2007). We used Enzo kit ADI-901-097 and followed the manufacturer's instructions, except that plasma was treated with 1% steroid displacement buffer and was diluted 1:40 with assay buffer prior to the assay. For study 1 the intra-assay coefficient of variation was 8.6% for a low control and 3.3% for a high control. Any value outside of the standard curve (*n* = 4) was set to the corrected sensitivity (1.37 ng/ml). For study 2 the intra-assay coefficient of variation was 9.1% for a low control and 3.2% for a high control.

Behavioral Analysis

Video cameras (Supercircuits, model PC182XS) were placed in the wind tunnel plenum to record feeding behavior (feeding duration as time spent at the food cup) and overall movement (total distance moved, time spent moving). Behavior was recorded during the time birds were housed in the plenum, but not when birds were housed in their environmental chambers. We recorded birds weeks 5 through 9 for s*tudy 1* and weeks 3 through 12 for *study 2*. Recording occurred for the first 5–6 h when birds were in the wind tunnel. To extract behavioral data, we used live tracking with Noldus EthoVision XT software using center-point detection settings to track each individual with static subtraction. The software analyzed total distance moved (cm) and cumulative duration of movement (s). The start velocity of movement was set to 3.01 cm/s which was independently verified for this project. We also analyzed cumulative duration spent in zone (s), and latency to first approach to zone (s), with the zone representing each individual food cup.

DNA Extraction and Genetic Sexing

We obtained a blood sample from each bird to genetically determine sex. Blood was smeared on filter paper and left to dry. Filter paper was individually stored in plastic card holders and frozen until further use. DNA was extracted using an ammonium-based protocol to salt out proteins, modified from Griffiths et al. (1998). The DNA concentration was quantified using a NanoDrop 2000 Spectrophotometer (Thermo Fisher Scientific) and diluted with 1 × TE to make a usable stock of 60 and 30 ng/ml for subsequent polymerase chain reactions (PCRs). In birds, females are the heterogametic sex (ZW) and males are the homogametic sex (ZZ). Detection of the W sex chromosome will determine the sex of the individual, thus the DNA sexing technique among birds targets the chromobox-helicase-DNA binding gene (CHD-W). We used P2 and P8 primers to amplify portions of the CHD-W and CHD-Z genes. The PCR reaction mixture consisted of 3 μl of genomic DNA, 1x PCR buffer, 2 mM MgCl2, 0.2 mM dNTP, 0.2 μM P2 and P8 primers, and 1 unit of Taq DNA polymerase. PCR thermal cycle conditions were 94°C for 1 min (initial denaturing), 40 cycles of 94°C for 30 s, 48°C for 45 s, and 72°C for 45 s, and 72°C for 5 min (final extension). PCR products were separated on a 3% agarose gel pre-stained with Sybersafe (S33102 Thermo Fisher Scientific) in 1x TAE buffer. The final gel electrophoresis showed two bands for females and one band for males.

Food Consumption

Food consumption was measured in *study 2* only. When the birds entered the wind tunnel plenum, we weighed each food cup for each bird to the nearest 0.1 g. After the birds were inside the wind tunnel for 24 h, we immediately weighed each food cup to determine the amount of food ingested. We assumed spillage of seed between each food cup would be small because the food cups had steep walls, and we observed very little food on the cage bottoms.

Statistical Analysis

Data were analyzed using linear mixed models in SPSS (IBM, Version 25.0). Fortnight (2 week period), experimental group, and their interactions were entered as fixed effects. To control for repeated measures, bird ID was entered as a random effect. Sex was omitted as only 4 individuals were female in the entire sample study (2 females in each study). Because the two studies were conducted a year apart, we analyzed their data separately.

RESULTS

Body Composition

There were different body composition responses between *studies 1* and *2*. In *study 1*, birds exposed to storm cues had higher fat mass content (**Figure 3A** and **Table 1**), lean mass content (**Figure 4A** and **Table 2**) and overall body mass (**Table 3**) compared to control birds.

In *study 2*, birds exposed to storm cues twice per week had lower fat mass content (**Figure 3B** and **Table 1**) compared to control, but we detected no difference in lean mass content (**Figure 4B** and **Table 2**) or overall body mass (**Table 3**). We did not detect any difference in fat, lean or overall body mass between fixed and unlimited food groups (see **Tables 1–3**). In *study 2*, experimental birds consumed more food than control birds (**Figure 5** and **Table 4**) and increased food consumption across time (**Figure 5** and **Table 4**). Food consumption was mot measured in *study 1*.

Corticosterone

In *study 1*, baseline corticosterone levels significantly decreased across time (**Figure 6A** and **Table 5**), however, no differences in baseline levels were observed between treatment groups (**Figure 6B** and **Table 5**).

Contrary to predictions in *study 2*, experimental birds had lower baseline corticosterone levels than control birds (**Figure 6B** and **Table 5**). Corticosterone levels also decreased across time (**Figure 6B** and **Table 5**), but there were no significant differences between food groups (**Table 5**).

Feeding Duration

In *study 1*, the time spent at the food cup was not affected by time or treatment (**Figure 7A** and **Table 6**).

In *study 2*, there was no difference in the total time spent at the food cup between birds receiving limited or unlimited food access (**Table 6**). Experimental birds spent more time feeding than control birds in the first 2 weeks of the study, then quickly reduced feeding duration to levels similar to those of control birds (**Figure 7B** and **Table 6**).

Total Movement

In *study 1* for fortnights 3 through 5, there were no significant effects on total distance moved across time (**Table 7**) or between treatment groups (**Table 7**). Thus, total distance moved was not affected by changes in barometric pressure or temperature.

In *study 2*, there were no differences between food group (**Table 7**) or treatment group (**Table 7**) in the distance moved, but the distance moved did increase across time (**Table 7**).

DISCUSSION

We analyzed physiological and behavioral responses, including corticosterone levels, body composition, feeding and overall behavior in white-throated sparrows exposed, or not exposed, to recurrent inclement winter weather cues once per week (*study 1*) or twice per week (*study 2*) and found noticeable differences between treatments. Birds that were repeatedly exposed to storm cues responded both physiologically and behaviorally, however, most responses did not match predictions.

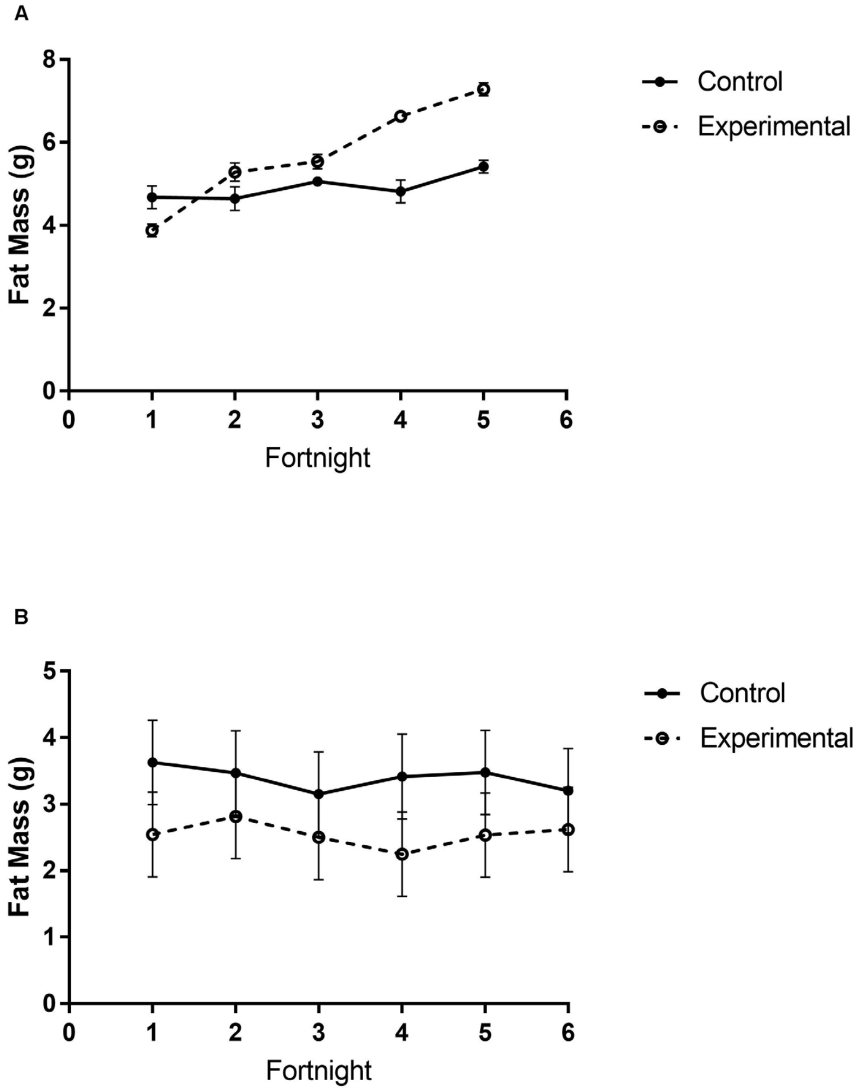

FIGURE 3 | Fat mass content of white-throated sparrows exposed to **(A)** low-frequency inclement weather conditions (study 1) or **(B)** high-frequency inclement weather conditions (study 2). **(A)** Experimental birds had higher fat mass content. **(B)** Control birds had higher fat mass content. Points indicate mean total mass values and error bars indicate SEM.

In s*tudy 1*, simulated winter weather cues once per week caused an increase in overall mass, lean mass, and fat mass. However, baseline corticosterone levels, the time spent feeding and overall movement while in the wind tunnel were not significantly different between groups. The cues associated with one simulated storm system per week were enough to elicit a physiological change in body composition, however, these cues did not appear to act cumulatively as a chronic stressor to induce a change in baseline corticosterone levels or behavior.

In contrast, in *study 2* we found that simulated winter weather cues twice per week caused lower baseline corticosterone levels and lower fat mass. There was no difference in lean mass or feeding duration between groups, however, experimental birds did ingest more food despite no detectable change in feeding duration. Birds thus increased their ingestion rate per time foraging (time at the food cup), rather than extending foraging time. These studies provide further evidence that birds can respond to changes in temperature and barometric pressure,

TABLE 1 | Fixed effects from the linear mixed effects model of fat mass in study 1 (indicated by 1) and study 2 (2) between treatment groups, food groups and across time.

Source	Numerator df	Denominator df	*F*	Sig.
1: Treatment group	*1*	*80*	*4.597*	*0.035*
2: Treatment group	*1*	*25.62*	*1.746*	*0.023*
1: Time	7	80	1.231	0.296
2: Time	6	116.165	0.051	0.822
2: Food group	1	22.77	0.102	0.752

Significant main effects are italicized.

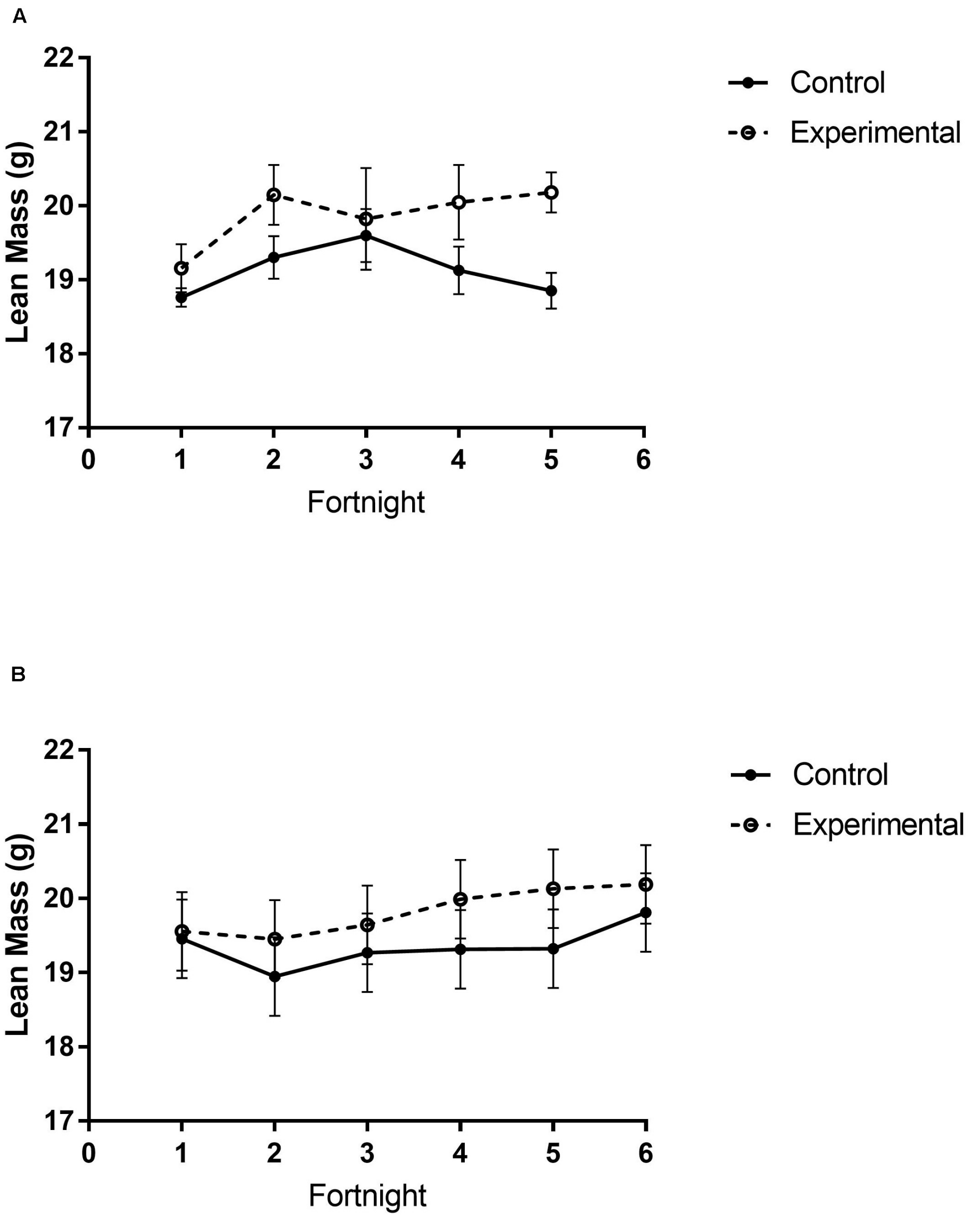

FIGURE 4 | Lean mass content of white-throated sparrows exposed to **(A)** low-frequency inclement weather conditions (study 1) or **(B)** high-frequency inclement weather conditions (study 2). **(A)** Experimental birds had higher lean mass content. **(B)** There were no differences in lean mass between groups. Points indicate mean total mass values and error bars indicate SEM.

but the frequency of simulated storm exposure can specifically influence how birds will respond.

Food Ingestion and Body Composition

Increasing fat stores is a common wintertime response to the onset of inclement winter weather to prepare against unpredictable future conditions and disruptions in resource availability (Carey and Dawson, 1999). We predicted that birds exposed to simulated storm cues should increase fat as an anticipatory response. Results from *study 1* were consistent with this prediction, but in *study 2* body fat was reduced in response to increased storm frequency. Interestingly, despite lower levels of fat, the amount of food ingested during the storm simulation was higher in experimental *study 2* birds. This suggests that although these birds were ingesting more food during simulated storm exposure, they were unable to allocate energy to creating additional fat stores. Increased energy storage is a common response to unpredictable or unfavorable conditions in birds (e.g., Kelly et al., 2002; van Berkel et al., 2018). Combined, these results suggest that in response to inclement weather cues birds will eat more and store more fat, but if the energetic demands of storms are too high, fat stores may be reduced below control conditions.

TABLE 2 | Fixed effects from the linear mixed effects model of lean mass in study 1 (indicated by 1) and study 2 (2) between treatment groups, food groups and across time.

Source	Numerator df	Denominator df	*F*	Sig.
1: Treatment group	*1*	*80*	*5.89*	*0.017*
2: Treatment group	1	22	0.029	0.866
1: Time	7	80	1.164	0.333
2: Time	6	116.114	2.702	0.757
2: Food group	1	22.18	0.516	0.480

Significant main effects are italicized.

TABLE 3 | Fixed effects from the linear mixed effects model of total body mass in study 1 (indicated by 1) and study 2 (2) between treatment groups, food groups and across time.

Source	Numerator df	Denominator df	*F*	Sig.
1: Treatment group	*1*	*80*	*8.911*	*0.004*
2: Treatment group	1	131	0.490	0.485
1: Time	7	80	1.203	0.304
2: Time	6	114.86	1.012	0.317
2: Food group	1	23.14	0.43	0.838

Significant main effects are italicized.

Unfortunately, we did not measure food consumption in *study 1*. Further research could titrate the points at which increased food ingestion is insufficient to support additional fat storage.

Increased thermogenic demand can cause increased lean mass to enhance thermogenesis (Carey et al., 1989) and shivering of the large flight muscles is the primary means of thermogenesis in most birds (Carey and Dawson, 1999). Through winter acclimatizing, flight muscles are often enlarged to facilitate shivering responses (Swanson, 2001). We thus predicted an increase in lean mass in birds exposed to storm cues. Similar to fat mass data, our prediction was partially met. Birds exposed to one simulated storm per week (*study 1*) had higher lean mass than controls, but this trend was not significant in birds exposed to two storms per week (*study 2*). Though lean mass appears to increase over time for experimental birds in both studies (**Figure 4**) this was not statistically significant.

The effects on body composition and food consumption indicate that exposure to a higher frequency of simulated storms per week may more negatively influence the birds' ability to store energy and exceed a threshold white-throated sparrows. Below the threshold the birds stored energy in fat and muscle tissue, but beyond the threshold energy may have been immediately invested in coping (higher metabolic rate) rather than being stored. It is possible that the birds were 'coping' with the higher rate of storms despite the lower fat reserves, as they did not have lower body mass in general and remained healthy. However, with lower energy stores the birds would certainly be more susceptible to future energetic challenges.

A previous study found that red knots (*Calidris canutus*) exposed to cold conditions increased their food ingestion, accompanied with increased body mass and lean muscle content to cope with cold conditions (Vézina et al., 2006), similar to the findings of our *study 1*. Captive dunlins (*Calidris alpina*), similarly, increased body mass following high winds and lower temperatures (Kelly et al., 2002). It appears that food ingestion, fat storage, and increased lean mass to enhance shivering are adaptive responses to inclement winter weather in birds, but that this response can be overcome by increased frequency of exposure to inclement weather cues. Although the experimental birds in *study 2* remained generally healthy, they were not able to increase energy reserves as did the birds in *study 1*. It is also possible that our birds in study 2 switched coping

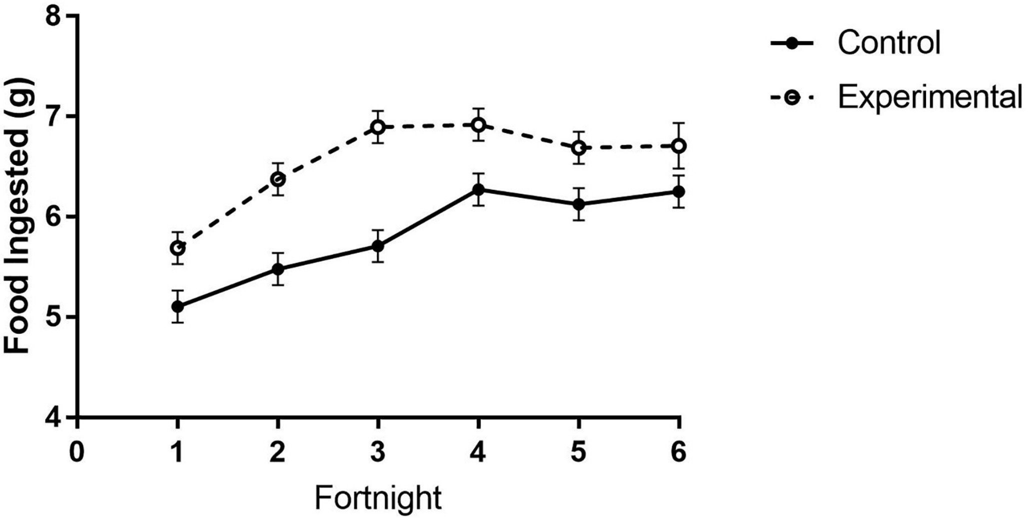

FIGURE 5 | Food consumption of white-throated sparrows in study 2 exposed to high-frequency inclement weather cues or control conditions. Birds that were repeatedly exposed to simulated high-frequency storm cues ingested more food than control birds. Points indicate mean food amounts ingested (g) and error bars indicate SEM.

strategy from energy storage to energy conservation through hypometabolism or hypothermia (McKechnie and Lovegrove, 2002). Such hypothermic responses can be modulated by food predictability (Nilsson et al., 2020). Because we did not measure metabolic rates in our study we cannot disentangle the potential mechanisms by which the birds in *study 2* coped with the experimental storm cues. Regardless, because they did not increase energy stores as did the birds in *study 1*, they would likely be less capable of meeting future energy demands or stressors.

Corticosterone

We predicted that repeated storm cue exposure may act cumulatively to create a chronic stressor that would result in elevated baseline corticosterone levels. This prediction was not met. In both studies, corticosterone levels decreased over time, potentially indicating that birds were habituating to housing conditions throughout the study. In *study 1* there were no detectable effects on corticosterone, replicating earlier studies showing that songbirds can respond to storm cues without modulating glucocorticoid levels (Breuner et al., 2013; de Bruijn et al., 2017). In contrast, in *study 2* we found lower corticosterone levels in birds exposed to inclement winter weather cues twice per week. Birds exposed to two simulated storms per week may lower corticosterone levels to conserve energy.

TABLE 4 | Fixed effects from the linear mixed effects model of food ingested between experimental groups and across time for study 2.

Source	Numerator df	Denominator df	*F*	Sig.
Treatment group	*1*	*504*	*45.917*	*<0.0001*
Time	*6*	*504*	*14.715*	*<0.0001*

Significant main effects are italicized.

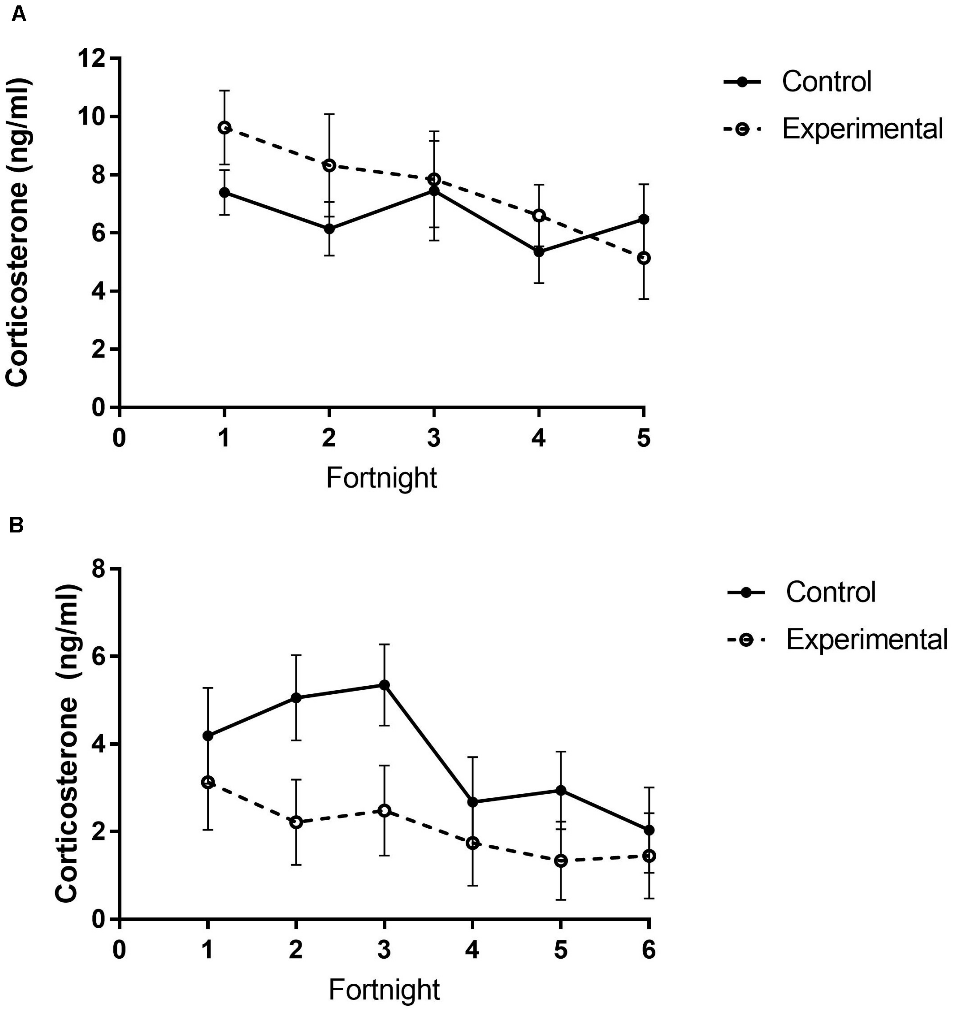

FIGURE 6 | Total plasma corticosterone of white-throated sparrows exposed to **(A)** low-frequency inclement weather cues (study 1) or **(B)** high-frequency inclement weather cues (study 2) compared to control conditions. **(A)** There were no differences in plasma corticosterone levels between treatment groups, but levels did significantly decrease across time. **(B)** Control birds had higher corticosterone levels and decreased levels across time. Points indicate mean corticosterone levels (ng/ml) and error bars indicate SEM.

TABLE 5 | Fixed effects from the linear mixed effects model of baseline corticosterone levels in study 1 (indicated by 1) and study 2 (2) between treatment groups, food groups and across time.

Source	Numerator df	Denominator df	*F*	Sig.
1: Treatment group	1	95.671	0.848	0.36
2: Treatment group	*1*	*55.575*	*4.098*	*0.048*
1: Time	*1*	*79.922*	*7.510*	*0.008*
2: Time	*6*	*88.313*	*12.575*	*0.001*
2: Food group	1	56.248	0.391	0.534

Significant main effects are italicized.

TABLE 6 | Fixed effects from the linear mixed effects model of time spent at the food cup in study 1 (indicated by 1) and study 2 (2) between treatment groups, food groups and across time.

Source	Numerator df	Denominator df	*F*	Sig.
1: Treatment group	1	24.680	1.494	0.233
2: Treatment group	1	21.003	2.39	0.137
1: Time	2	80.938	0.057	0.945
2: Time	*4*	*344.15*	*8.75*	*0.003*
2: Food group	1	20.63	0.21	0.65
*2: Food group * Time*	*4*	*344.07*	*12.09*	*<0.0001*

Significant main effects are italicized.

TABLE 7 | Fixed effects from the linear mixed effects model of total distance moved in study 1 (indicated by 1) and study 2 (2) between treatment groups, food groups, across time and their interactions.

Source	Numerator df	Denominator df	*F*	Sig.
1: Treatment group	1	64	0.002	0.97
2: Treatment group	1	39.275	0.665	0.420
1: Time	4	64	1.237	0.31
2: Time	*6*	*353.442*	*17.417*	*<0.0001*
2: Food group	1	39.569	0.094	0.761

Significant main effects are italicized.

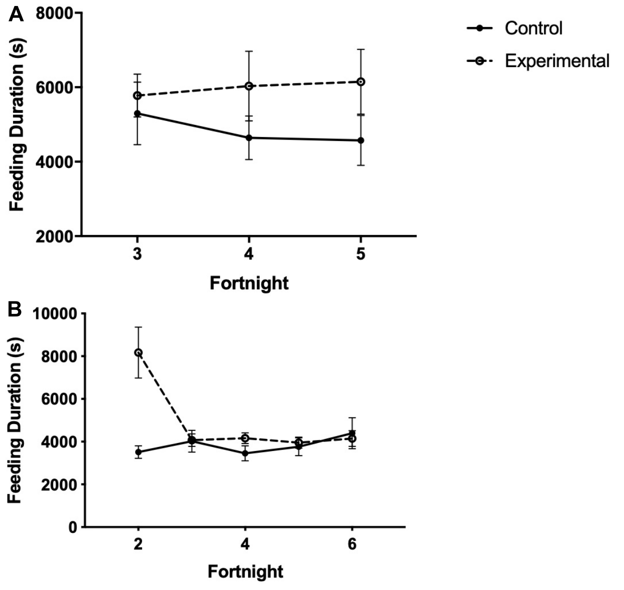

FIGURE 7 | Feeding duration (time spent at the food cup) in seconds of white-throated sparrows exposed to **(A)** low-frequency inclement weather conditions (study 1) or **(B)** high-frequency inclement weather conditions (study 2). Points indicate total time spent feeding (s) and error bars indicate SEM.

This may represent a downregulation of the HPA axis under chronic stress conditions (de Bruijn et al., 2017). Indeed, the relationship between environmental stressors and baseline corticosterone levels is not as established as some studies suggest. HPA function, including the directional changes of glucocorticoid concentration, can differ widely across species exposed to repeated stressors and chronic stress (Dickens and Romero, 2013). A response in HPA function itself is more informative than the actual direction of that change (e.g., increasing or decreasing glucocorticoid levels; Dickens and Romero, 2013). Further work, perhaps using ACTH and dexamethasone challenges to characterize HPA function, would be required to better determine how birds are altering corticosterone regulation in response to twice weekly storm cues.

Behavioral Response

In the winter, a low pressure cold front can bring precipitation in the form of snow through most of white-throated sparrows' wintering range. Since these birds are ground feeding species, they need to forage prior to the onset of the storm as food may become less available once the ground is covered in snow. Previous studies that experimentally decreased barometric pressure found that birds decreased their latency to feed and increased the feeding amount (Breuner et al., 2013; Metcalfe et al., 2013). We therefore predicted that foraging time should increase in birds exposed to simulated inclement weather.

We found no group differences in overall activity (as measured by total movement). However, in *study 2* birds exposed to storm cues twice per week spent more time at their food cup during the first 2 weeks of the study, regardless of whether they received a fixed amount of food per day or unlimited food. This was reflected in the total mass of food consumed during the manipulation (see above; **Figure 5**).

Increased levels of corticosterone can lead to an increased rate of foraging (Breuner and Hahn, 2003), however, this direct relationship was not observed in this study. Experimental birds showed lower corticosterone levels but did increase their feeding duration and food ingestion, indicating that there was still a response as a result of repeated storm cues, but these repeated storm cue exposures did not act as a stressor to induce an HPA response. Interestingly, a limited or unlimited diet did not influence any behavioral or physiological responses. Captive white-crowned sparrows showed little activity around their food cups when food was unlimited, but activity at the food cup increased once food was removed (Astheimer et al., 1992). Similarly, European starlings (*Sturnus vulgaris*) increased foraging time when food was experimentally made unpredictable (van Berkel et al., 2018). Whether birds in *study 2* had unlimited or limited food amounts, they were still consistently exposed to food, therefore there may not have been a strong response to immediately forage once environmental changes were detected due to the predictability of resources. *Study 2* birds exposed to storm cues ingested more food and spent more time feeding but had lower fat mass content and corticosterone levels. This indicates that the rate of feeding may have been higher and more intense when birds were at the food cups. Although feeding duration and ingestion increased in experimental birds, we did not detect more fat mass in these individuals, indicating the frequency of storm cues occurring may have affected how food was stored and metabolized after ingestion. The increase in food consumption may be a result of immediate thermogenesis costs. Wintering songbirds can rapidly increase summit metabolic rates during exposure to chronic cold conditions (Stager et al., 2020). The sparrows in *study 2* may have similarly been using energy to increase metabolic rates rather than storing energy as fat.

CONCLUSION

The responses of birds exposed to simulated storms twice per week for 12 weeks compared to once per week for 9 weeks were remarkably different. These results suggest birds can detect changes in temperature and barometric pressure and can adjust their response accordingly, however, there may be a threshold of storm frequency to which birds are able to cope, both metabolically and physiologically. Our findings suggest that increasing the frequency of storm exposure from once per week to twice per week may exceed a threshold for these songbirds. On one side of the threshold birds respond to storm cues by storing energy, and on the other they must immediately expend energy to maintain homeostasis such that they are unable to invest in energy storage, likely putting them at risk to future stressors.

DATA AVAILABILITY STATEMENT

Data are available at Data Dryad https://doi.org/10.5061/dryad.69p8cz8zk.

ETHICS STATEMENT

All procedures were approved by the University of Western Ontario's Animal Care Committee and followed the guidelines of the Canadian Council for Animal Care.

AUTHOR CONTRIBUTIONS

AB conceived the idea, conducted the experiments, and wrote the manuscript. SM-S substantially contributed to the experimental design and edited the manuscript. All authors contributed to the article and approved the submitted version.

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Shifting Breeding Phenology in Eurasian Kestrels *Falco tinnunculus*: Effects of Weather and Urbanization

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Human-induced climate change and the destruction of natural habitats are two of the main threats to biodiversity worldwide. Animals can use local weather conditions as environmental cues for optimal breeding conditions, but climate change can cause severe phenological mismatches. Migratory species that have a shorter time period for their settlement decision, or species that breed in heavily transformed habitats, might be specifically sensitive to such change. Here, we analyzed the arrival and egg-laying dates of Eurasian kestrels (*Falco tinnunculus*) in Vienna (415 km^2), Austria, gathered by academic and citizen scientists between 2010 and 2018. To identify critical time windows in which weather variables affect phenology, we used a sliding window approach and considered the degree of urbanization as an additional predictor to unravel habitat-dependent relationships. Furthermore, we assessed the relationship between arrival and egg-laying (i.e., the length of the time gap in-between). We found that arrival dates were not influenced by urbanization, and that egg-laying started earlier in drier weather conditions prior to arrival, and earlier in more natural areas than in the urban center. The time gap between arrival and egg-laying was slightly shorter in breeding pairs that arrived later at their nest sites. Our results might indicate a strategy to mitigate later arrival by relatively earlier egg-laying through reducing the length of the courtship period. Such a behavioral adaptation could avoid negative effects of a later onset of breeding on their reproductive success, which is known from previous studies in our urban population.

Keywords: urban ecology, timing of breeding, citizen science, urban gradient, urban raptor, bird migration, direct assessment hypothesis, sequential settlement

INTRODUCTION

Human-induced rapid environmental change (Sih, 2013), such as climate change and destruction of natural habitats, threatens biodiversity globally, posing new challenges throughout all habitats and from the species to community level (Pimm and Raven, 2000; Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Hendry et al., 2017). Due to the continuous growth of human populations and associated resource use (Vitousek, 1994), both climate and land-use change are expected to intensify further within this century (Sala et al., 2000). In fact, the United Nations Secretariat considers climate change and land-use change in form of urbanization to be the most significant sources of global environmental change (United-Nations, 2019).

One key mechanism induced by global change is phenological shift, i.e., an altered timing of seasonal life cycle activities or events (Walther et al., 2002), which influences animal reproduction and population viability (Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003; Parmesan, 2006; Jetz et al., 2007; Møller et al., 2008; Visser et al., 2012). These shifts might be caused by changing abiotic factors, for instance, snowmelt affecting the flowering of plants (Inouye, 2008), but also entail biotic interactions (Miller-Rushing et al., 2010). However, phenological shifts can be positive or negative. For example, earlier springs and longer frost-free seasons with reduced snowfall advance flowering of plants and egg-laying in birds (Zohner, 2019), which might promote the exploitation of newly available resources (Miller-Rushing et al., 2010) with associated fitness advantages. On the other hand, such shifts can cause temporal mismatches between trophic levels, e.g., plants and pollinators or predators and prey (Stenseth and Mysterud, 2002; Edwards and Richardson, 2004; Visser and Both, 2005; Visser et al., 2006; Both et al., 2009; Renner and Zohner, 2018). In urban surroundings, phenological shifts could be exacerbated by the urban heat island effect (Oke, 1982; Streutker, 2003) as urban core areas across the globe have consistently higher ambient temperatures and less pronounced fluctuations in diel temperatures than their adjacent non-urban areas (reviewed by Arnfield, 2003). Many bird species breeding in urban areas respond with an advanced reproductive phenology, e.g., laying earlier than their non-urban conspecifics (Deviche and Davies, 2014).

The seasonality of the environment restricts time windows suitable for reproduction or growth of organisms (Visser and Both, 2005). For breeding birds, the question of when and where to breed determines their own and their offspring's fitness (Daan and Tinbergen, 1997). Although birds are highly mobile, they are inherently dependent on their imminent surroundings as soon as they start breeding. To optimize reproduction, birds need to time the hatching of their young as close to the environmental optimum as possible, but they need to initiate the breeding process well before this environmental optimum occurs (Perrins, 1970; Daan et al., 1989). Consequently, predictions of ideal conditions – especially the sufficient availability of suitable food to raise offspring – are based on environmental (Baker, 1938; Murton and Westwood, 1977; Wingfield, 1983) but also social cues at the time before breeding ['conspecific attraction' (Stamps, 1994) or 'public information hypothesis' (Danchin et al., 1998; Doligez et al., 2003)].

Long-term environmental predictors for breeding birds of the temperate zone are photoperiodical cues (reviewed by Sharp, 1996). But the longer the time gap between the perception of the cue(s) and the fitness consequences, the higher the probability of mismatches (Padilla and Adolph, 1996). This becomes even more challenging in a severely altered environment, such as urban core areas, because here species face different environmental conditions than they experienced in the fitness landscape they evolved in (Tilman and Lehman, 2001).

To adjust the fine-tuning to local conditions, additional factors closer to the actual onset of breeding might be important predictors to find the environmental optimum (Visser et al., 2010), especially spring temperatures [i.e., less than 1 month before egg-laying; see review (Williams et al., 2015)]. Getting the timing right matters, because earlier clutches have more eggs, higher hatching and fledging rates and earlier broods are more likely to recruit into the breeding population (Perrins, 1970; Verboven and Visser, 1998; Grüebler and Naef-Daenzer, 2010; Sumasgutner et al., 2016; Harriman et al., 2017). The fitness advantages of earlier broods can be attributed to the quality of the environment, which naturally deteriorates as the season advances ['date hypothesis' (Perrins, 1970); see also reviews of Verhulst and Nilsson (2008) and Harriman et al. (2017)], and to the individual quality of the parents, enabling an earlier increase of the female's fitness toward breeding condition ['quality hypothesis' within the Ideal Dominance Distribution or Ideal Despotic Distribution (Fretwell, 1972), e.g., through superior hunting skills of the male, body condition of the female, quality of the occupied territory, and previous breeding experience (Perrins, 1970; Drent and Daan, 1980; Newton, 1980; Chastel et al., 1995; Forslund and Pärt, 1995; Daunt et al., 1999; Kokko, 1999; Sergio et al., 2007)]. Parents may have to face a trade-off considering breeding benefits (which might be related to the date hypothesis) as well as fitness costs (which might be related to the quality hypothesis) associated with the timing of breeding (Verhulst and Nilsson, 2008; Grüebler and Naef-Daenzer, 2010). Similarly, earlier-arriving individuals in migratory species are usually fitter than later-arriving ones, which settle on progressively lower-quality territories ('sequential settlement'; Sergio et al., 2007).

One species that appears intrinsically resilient to urbanization and even proliferates in human-modified environments is the Eurasian kestrel *Falco tinnunculus* (hereafter 'kestrel'). In this study, we analyze long-term data (2010–2018) on arrival from wintering grounds and the timing of breeding from the kestrel population in Vienna, Austria. The kestrel is the most common raptor species of the Palearctic region (Ferguson-Lees and Christie, 2005) and Vienna holds the highest density of non-colonial breeding individuals (Wichmann et al., 2009; Sumasgutner et al., 2014a). In natural areas, kestrels mainly breed in deserted or usurped corvid nests or in cliff cavities (Village, 1990), but they opportunistically use anthropogenic structures available in agricultural areas (Costantini et al., 2014; Sumasgutner et al., 2019b) and urban settings (Kübler et al., 2005; Sumasgutner et al., 2014a,b). If voles, which are the kestrel's main prey, decline in availability due to natural cycles (Korpimäki, 1986; Valkama et al., 1995) or become less available due to urbanization (Sumasgutner et al., 2014a), kestrels adjust by broadening their diet width and hunting habitat (Korpimäki, 1986; Valkama et al., 1995; Kübler et al., 2005; Mikula et al., 2013;

Sumasgutner et al., 2013; Kreiderits et al., 2016) and by increasing hunting effort and enlarging hunting areas (Riegert et al., 2007a,b). Consequentially, there is a strong implication that kestrels are urban adaptors.

Previous studies showed that weather parameters during winter, arrival and courtship affect breeding productivity of kestrels in Vienna; higher precipitation in winter and also spring rainfall reduces productivity, probably due to delayed egg-laying (Kreiderits et al., 2016). In Mediterranean kestrels, dry and mild winters reduce breeding productivity, but at the same time higher spring rainfall delays egg-laying dates (Costantini et al., 2010b), indicating that different breeding stages are sensitive to different time-windows. Thus, it remains a worthy endeavor to identify which weather predictors are the most relevant during which period throughout the breeding cycle. Besides photoperiodism, these critical time windows might be additional cues for settlement decisions, hence, having a significant effect on the reproduction of kestrels in general and explaining large-scale variation of egg-laying dates within the Western Palearctic (Meijer et al., 1992; Carrillo and González-Dávila, 2009). However, if photoperiodism is the sole predictor, an adaptive response to global change would be heavily limited.

In this study we first (i) determine the critical time window(s) (start and duration) and key weather variables which predict egg-laying dates of kestrels in Vienna. We expected the critical time window(s) to coincide with the winter before breeding, arrival and the courtship period. This could be evident in either (a) several shorter critical time windows, or (b) one long critical time window starting before arrival and ending during courtship. We furthermore expected precipitation to be the strongest predictor with a larger effect in more natural compared to urban nest sites as cavities in buildings might provide better shelter than open nests. A similar assessment of the arrival time at the nest site after migration was not possible due to the lack of information where kestrels of the study population overwinter.

Second (ii), we investigate if the onset of breeding is determined by the arrival time itself. This would be the case if courtship duration (time gap from arrival until egg-laying) stays constant from early to late arrivals. Alternatively, egg-laying could be relatively earlier (shortening time gap) or relatively later (elongating time gap). Shortening of time gaps could indicate a strategy of mediating later arrival (and thus avoiding potential related fitness costs of living in urban environments for the parents) by a relatively earlier onset of breeding. Contrary, late arrival could result in an increased time gap between arrival and egg-laying due to worsening environmental conditions for reproduction over the course of the breeding season. Furthermore, these time gaps could vary depending on the degree of urbanization. For example, a shorter time gap at the most urbanized nest sites would indicate that the females reach breeding condition earlier in an urban setting than in suburban areas at the city's periphery.

Our final objective was to build a global model to predict arrival time and egg-laying dates to gain a deeper understanding of the ecological processes shaping the population dynamics of kestrels along an urbanization gradient.

MATERIALS AND METHODS

Study Species

The population density of kestrels in Vienna ranges between 89–122 breeding pairs/100 km^2 (Sumasgutner et al., 2014b) and is relatively high compared to previously published estimates [60–96 breeding pairs (bp)/100 km^2; Wichmann et al., 2009], densities reported in other European cities [e.g., 22.9–33.3 bp/100 km^2 in Berlin, Germany (Kupko et al., 2000) or 40–55 bp/100 km^2 in Paris, France (Malher et al., 2010)], and rural areas in Austria with 8–30 bp/100 km^2 (Gamauf, 1991). Kestrels are considered partial migrants with a post-breeding migration that varies immensely with latitude (Village, 1990) and starts in September/October (Holte et al., 2016). It is yet unclear where the kestrel population of Vienna is migrating to. Unlike populations studies in other European cities (Romanowski, 1996; Riegert and Fuchs, 2011), kestrels in Vienna disperse in mid-summer and temporarily leave the city during winter (Sumasgutner et al., 2014a). Only a few, primarily male individuals are known to spend the winter within urban areas of Vienna (Sumasgutner et al., 2014b). Within Europe, females and juveniles travel larger distances than males and adults (Terraube et al., 2015). In Vienna, inner-city territories were occupied slightly before territories in more natural areas in 2010 and 2011, indicating a preference for inner-city nest sites (Sumasgutner et al., 2014a).

Study Area and Urbanization Gradient

Vienna (48°12′N, 16°22′E, 150–500 m a.s.l., 415 km^2, 1.91 million inhabitants), the capital of Austria, is considered a 'green' city with approximately 50% of the total area being urban green space. We quantified a soil seal factor (SSF) as percentage of impervious/sealed surfaces within a buffer circle of r = 500 m (78.5 ha) around each nest site, corresponding to the lower end of kestrel hunting area sizes reported from Kiel, Germany (range of 90–310 ha; Beichle, 1980) and České Budějovice, Czech Republic (range of 80–2,500 ha; Riegert et al., 2007b). We chose the smaller scale for our home-range level urbanization score, as high densities (such as in kestrels in Vienna) usually result in smaller home range sizes in urban raptors (e.g., Dykstra et al., 2001; Rutz, 2006; Dykstra et al., 2018). The SSF was our proxy for an urbanization gradient. We excluded rural areas, defined as areas with SSF < 1%, which mainly consist of larger agricultural, forest and conservation areas located within the cities' boundaries, thus limiting the study area to 243 km^2.

The SSF was calculated using ArcMap (ESRI Inc., 2017) from land allocation maps provided by the Environmental Protection Bureau of Vienna. These maps indicated 51 different land cover categories, which were summarized into impervious/sealed and unsealed surfaces (**Figure 1**). 35 land cover categories, such as buildings, roadways, pavements or parking lots, were assumed to be sealed surfances. The remaining 16 land cover categories like unsealed yards, grasslands, forests, agricultural areas, wine yards, cemeteries, gravel pits and various sorts of water bodies

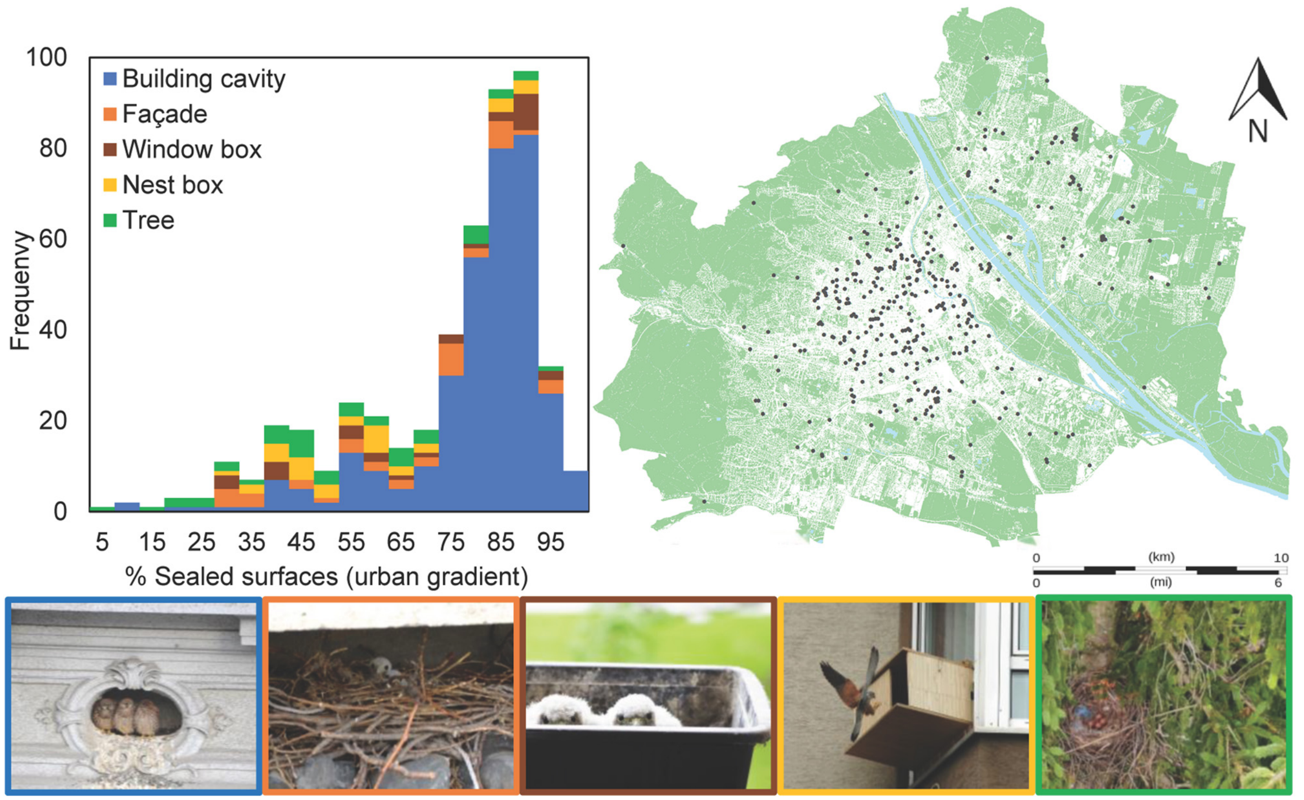

FIGURE 1 | (Left) Distribution of nest types along the urban gradient (n = 484, 2010–2018): roof openings or other building cavities (66%), corvid nests on the façade (7%) or in trees (8%), window boxes (6%) and specifically provided nest boxes (6%). **(Right)** Location of nest sites monitored by citizen science community (occupied in at least 1 year; n = 366; gray points). Water bodies in blue, sealed surfaces in white and greenspace. **(Below)** Building cavity ©C Hofmann, corvid nest in façade ©M Graf, window box ©P Sumasgutner, nest box ©GF Witting and corvid nest in tree ©SC McPherson.

were classified as unsealed soil (**Supplementary Table S1**). Since the land allocation maps are renewed within periods of 4 years, the SSF was calculated based on one map that was digitized between 2010 and 2013 for all nest sites occupied before 2014 and on a map that was digitized between 2014 and 2017 for all other nest sites. Thus, some nest sites which were occupied by kestrels in both time periods were attributed with two different SSFs respective to the year observed. The SSF of all observed nest sites ranged from 4.77 to 98.52%.

The Monitoring Program

The population has been monitored systematically since 2010 and incorporated systematic observations by academic scientists, data contributed by ornithologists involved in breeding-bird surveys and citizen science data reported by phone, e-mail, social media, or via BirdLife Austria and the online platform bird.at. The contribution of each citizen varied strongly in extent and quality. While plenty of citizens did not report observations repeatedly, various contributors became a distinctive part of the project, reliably reporting on the arrival and reproduction at "their" nest site season after season. Often comprehensive pictures of the brood were provided. All reports were documented and notifications of (yet) unknown contributors without any supporting footage were verified *in situ* by academic scientists.

The following analyses include all data reported from 2010 to 2018 by academic and citizen scientists. Arrival and egg-laying dates were extracted from the notes taken by academic scientists and, if necessary, backed up by revising written communication with contributing citizens. Several citizen scientists stated when they first observed the kestrels at their nest upon return from their wintering grounds. As kestrels show very prominent behavior at the nest site, we assumed the time gap between arrival at the nest site and first notice by the citizens to be quite short. In case no specific arrival date was reported, the first date of correspondence with the citizen scientists was used as a substitute.

Several nest sites in Vienna offer a direct view from buildings located vis-à-vis, facilitating surveys without nest disturbance. Nesting in flower boxes on windowsills easily allows for daily nest checks. However, several nest sites cannot be seen from a vantage point and can only be accessed via attics or façades, by climbing trees or with the help of the Vienna Fire Fighters, who supported the monitoring program since its very beginning. Observations from the ground can give relevant cues on phenology but cannot be as precise as direct nest checks. In 7 of 9 years of the monitoring program, nestlings of accessible nests were at least examined once, measured and ringed which allowed an age estimation based on morphometric measurements and a backdating of the hatching and egg-laying dates (Kostrzewa and

Kostrzewa, 1987, 1993). Therefore, the egg-laying date was either observed directly, or deduced by calculating 30 days back from the observed or estimated hatching date (Village, 1990). We further specified if observations on the breeding stage were based on a direct assessment or citizen scientists.

Weather Data

Data on temperature and precipitation were obtained from the Central Institute for Meteorology and Geodynamics (ZAMG) as well as the Tutiempo Network, S.L. Both provide data from the weather station 'Vienna inner-city,' which is located in the 4th district of Vienna, 1.3 km from the center. Four different weather variables were analyzed separately: daily (24 h) average (T_{ave}), maximum (T_{max}) and minimum temperature (T_{min}) (all given in°C), and daily total precipitation (PP, given in mm).

Statistical Analysis

All statistical analyses were performed in R 3.6.1. (R Development Core Team, 2020). Confidence intervals were set to 95% and significance is referred to as $P \leq 0.05$. Arrival and egg-laying dates were processed as Julian days and followed a normal distribution. Of all recorded arrival dates, dates before the 1st of February and after the 21st of June were excluded (n = 11). Dates before 1st of February were likely to refer to males over-wintering in Vienna; dates after 21st of June were rare statistical outliers, which are likely to result from relocations after nesting failure.

In 2013 and 2018, we did not have a team member dedicated to correspond with our citizen scientists from the beginning of the breeding season as in other years, thus, data from these 2 years were excluded from the model on arrival dates (n = 3 each), leaving 515 observations to be analyzed (**Supplementary Figure S1**, left). For egg-laying dates, years 2016 and 2018 were excluded ($n_{2016} = 0$, $n_{2018} = 6$) as no banding (with age-assessment of offspring) took place, leaving n = 114 observations to be analyzed (**Supplementary Figure S1**, right). Additionally, arrival and egg-laying dates were documented at the same nest and within the same year in 68 cases, thus allowing for an exact assessment of the time gap between arrival and egg-laying (Δ Days). These observations (hereafter 'corresponding observations') were obtained irregularly in the years 2010–2012, 2014–2015, and 2017–2018.

To test hypothesis (i) and determine the time window(s) during which weather variables affect egg-laying dates (and hence, kestrels are sensitive to weather conditions), we followed a sliding window approach (Brommer et al., 2008; Williams et al., 2015). For this purpose, multiple Pearson's correlations were calculated for the annual mean egg-laying dates and the average of weather variables for various alternative time windows (**Figure 2**). We chose the length to vary between 1–90 days and tested every possible time window within a period starting 90 days before the mean annual laying date (n = 29295 Pearson's correlations). We performed the sliding window approach for each weather variable separately and calculated R^2 values from the Pearson's correlations.

To test if (ii) the onset of breeding was already determined by the arrival time itself, we used the data set of corresponding observations mentioned above and performed a linear regression with Δ Days as dependent variable and arrival date as an independent variable, using the lm() command in the base package (R Development Core Team, 2020).

We calculated linear mixed-effect models (LMMs) via maximum likelihood with a Gaussian error distribution. We used the Julian date of arrival or egg-laying as a response variable, and fitted nest ID (as a random term), observer category (as fixed factor in two levels: 'academic scientist' *versus* 'citizen scientist'), year of observation (as fixed factor), and SSF (as continuous fixed effect). For the model on egg-laying dates, we integrated the two most informative weather variables within the optimal time window assessed in (i). The arrival date was considered as an additional continuous fixed effect when working with the data set of corresponding observations.

All LMMs were built with lmer() in the package lme4 (Bates et al., 2015). Additionally, the packages LMERConvenienceFunctions (Tremblay and Ransijn, 2015) and car (Fox and Weisberg, 2019) were used for model validation by visual inspection of residuals. The conditional R^2-values [hereafter 'R2LMMc'; (Nakagawa et al., 2017) of the models were calculated with r.squaredGLMM() of the MuMIn package (Bartoń, 2016); significance of explanatory terms was assessed using their partial (Type III) significance values (χ^2-tests)]. For data visualization, the additional packages ggplot2 (Wickham, 2009) and ggpubr (Kassambara, 2018) were used. Effect plots were made using the package lattice (Sarkar, 2008).

RESULTS

Time Windows and Weather Variables Affecting Egg-Laying Date

Precipitation (PP) and maximum daily temperature (T_{max}) proved to be the most informative weather variables with the highest explanatory capacity (**Figure 3**), while average daily temperature (T_{ave}) was ranked second and daily minimum temperature (T_{min}) appeared to be least informative (**Supplementary Figure S2**). For PP, we found several, partly overlapping critical time windows. Two patterns could be derived from the critical time windows (**Figure 3**). First, time windows incorporating data from the last 3 weeks before mean egg-laying showed little explanatory capacity, whilst windows ending about 20 days before the mean annual laying date had high R^2-values (>0.5) but varied in position and length. Second, time windows of more than 3 weeks length which started from around 80 days before egg-laying were more informative, having R^2-values > 0.5. Highest R^2-values were recorded where the time windows of the two patterns were identical, with the maximum R^2 = 0.82 associated with a time window of 58 days duration, starting 79 days (approx. 11 weeks) and ending 21 days (3 weeks) before egg-laying. Within this time window, PP was correlated with egg-laying date in a way that higher

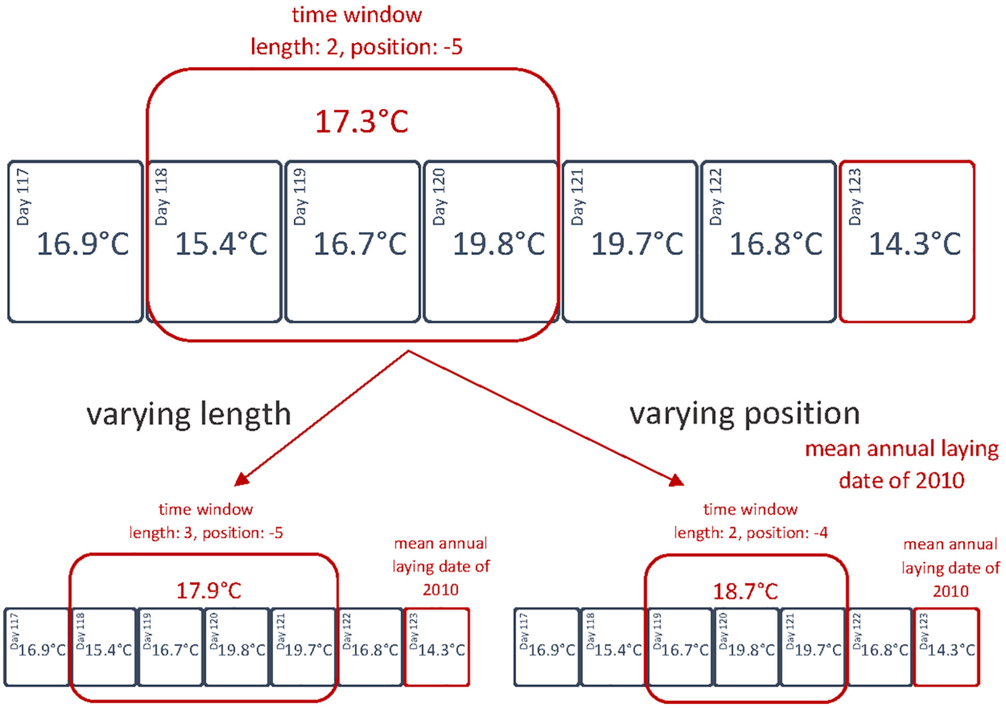

FIGURE 2 | Illustration of the sliding window approach in 2010 for the daily average temperature. Each time window is defined by its length (in nights, therefore 0 includes 24 h) and position (starting point in days, with the mean annual laying date being day 0).

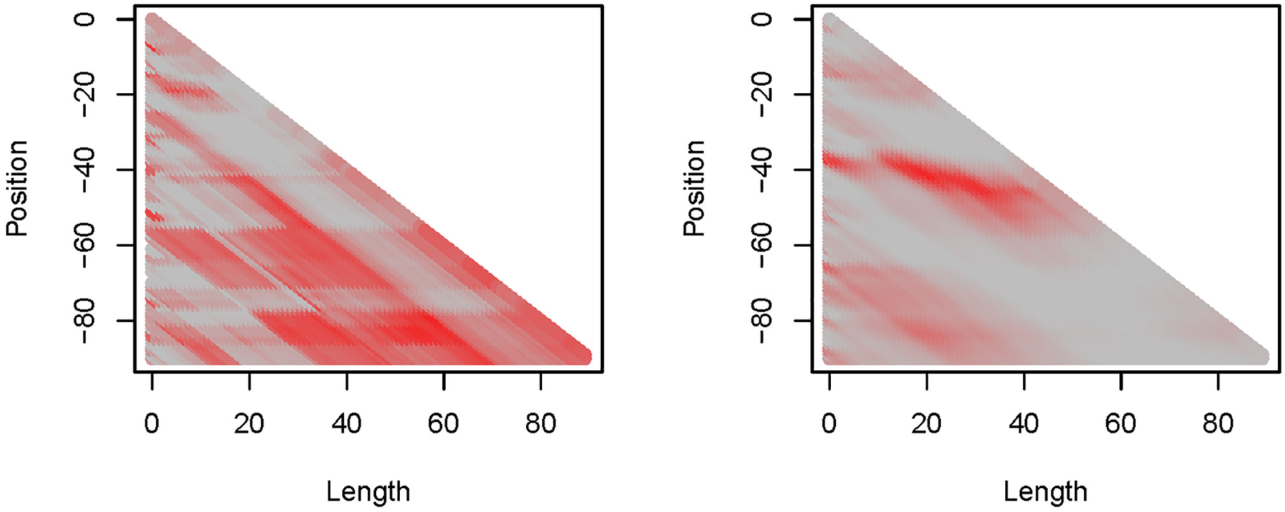

FIGURE 3 | Depiction of R^2-values derived by the sliding window approach on **(left)** precipitation (PP) and **(right)** daily maximum temperature (T_{max}). Both show a maximum R^2 = 0.82: PP at length = 58 and position = –79 (approx. 11–3 weeks before egg-laying), T_{max} at length = 20 and position = –40 (approx. 6–3 weeks before egg-laying).

precipitation corresponded with later egg-laying [$R_{(5)}$ = 0.90, P = 0.005].

For T_{max}, fewer critical time windows and fewer patterns were found compared to PP (**Figure 3**). Time windows of about 20 days that started approximately 1 month before egg-laying were most informative. The maximum R^2 = 0.82 was assigned to a time window of 20 days duration, which started 40 days and ended 20 days before egg-laying. During this time window, T_{max} was negatively correlated with later egg-laying dates [$R_{(5)}$ = −0.90, P = 0.005]. Among the other weather variables T_{min} had the lowest R^2-values [max. R^2 = 0.63; $R_{(5)}$ = 0.79, P = 0.034] and T_{ave} reached a maximum informative value of

$R^2 = 0.71$ [$R_{(5)} = -0.84$, $P = 0.017$]. All temperature parameters (T_{min}, T_{max}, and T_{ave}) were highly positively correlated with each other [T_{min} vs. T_{max}: $r_{(1258)} = 0.93$, $P < 0.001$; T_{min} vs. T_{ave}: $R_{(1258)} = 0.97$, $P < 0.001$; T_{max} vs. T_{ave}: $R_{(1258)} = 0.98$; $P < 0.001$].

Arrival Date and Environmental Conditions

For arrival dates, we fitted SSF, observer category and year as fixed effects and nest ID as a random term (**Table 1A**; R^2LMMc = 0.21). Year [$\chi^2_{(6,515)} = 27.94$; $P < 0.001$] and observer category [$\chi^2_{(1,513)} = 3.95$; $P = 0.047$] were significant (**Figure 4**). The estimates on arrival dates varied from 6.24 to −4.50 days between years, with the earliest reports in 2017 and the latest in 2011. The mean arrival date determined by citizen scientists was day 97.1 ± 15.1 (7th of April; $n = 319$), whereas the mean arrival date ascertained by academic scientists was day 103.2 ± 12.9 (13th of April; $n = 194$). Thus, citizen scientists reported arrivals on average 1 week earlier. SSF did not significantly affect arrival dates [$\chi^2_{(1,509)} = 1.36$; $P = 0.243$].

Egg-Laying Date and Environmental Conditions

There was no co-linearity between PP and T_{max} within the critical time windows [$r_{(n = 209)} = 0.12$; $P = 0.062$], hence, both were fitted into the same model. SSF and observer category were additional co-variates and nest ID was fitted as a random term (**Table 1B**, R^2LMMc = 0.77). Significant explanatory terms were PP [$\chi^2_{(1,211)} = 140.29$; $P < 0.001$], T_{max} [$\chi^2_{(1,211)} = 239.74$; $P < 0.001$], SSF [$\chi^2_{(1,206)} = 4.03$; $P = 0.045$], observer category [$\chi^2_{(1,209)} = 7.14$; $P = 0.008$], and year [$\chi^2_{(6,211)} = 60.10$; $P < 0.001$]. While year had an ambivalent effect, observations by academic scientists and higher PP, T_{max}, and SSF were positively correlated with later egg-laying dates (**Figure 5**). The mean egg-laying date reported was day 122.4 ± 19.2 (2nd of May; $n = 30$) for citizen scientists and day 123.8 ± 14.2 (4th of May; $n = 179$) for academic scientists, but note the unbalanced sample size.

TABLE 1 | LMMs on arrival dates (years 2010–2012 and 2014–2017) and egg-laying dates (years 2010–2015 and 2017), exploring the effects of Soil Seal Factor (SSF), observer category (academic vs. citizen scientist), year and, in the final model on egg-laying dates, precipitation (PP, daily precipitation mean from 21 to 79 days before the egg-laying) and maximum temperature (T_{max}, daily maximum temperature mean from 20 to 40 days before the egg-laying date).

	Estimate	SE	χ^2	P	Sign.	R^2 LMMc
(A) Arrival date ∼ SSF + observer + year + (1 | nest ID)						0.21
SSF	−0.04	0.03	1.36	0.243	–	
Observer category‡			3.95	0.047	*	
Academic scientist	3.49	1.76				
Year†			27.94	<0.001	***	
2011	6.24	1.92				
2012	5.55	3.75				
2014	0.73	2.60				
2015	5.64	2.50				
2016	3.92	3.98				
2017	−4.50	2.53				
Intercept	98.74	2.57	1476.05	<0.001	***	
(B) Egg-laying date ∼ PP + T_{max} + SSF + observer + year + (1 | nest ID)						0.77
PP	23.47	1.98	140.29	<0.001	***	
T_{max}	2.62	0.17	239.74	<0.001	***	
SSF	0.05	0.02	4.03	0.045	*	
Observer‡			7.14	0.008	**	
Academic scientist	4.33	1.62				
Year†			60.10	<0.001	***	
2011	1.25	2.09				
2012	1.97	1.88				
2013	11.01	2.13				
2014	−4.69	2.11				
2015	−0.45	2.09				
2017	−1.13	2.49				
Intercept	50.59	3.74	182.78	<0.001	***	

*We assessed the significance of explanatory terms using their partial (Type III) significance values (χ^2-tests). ‡Observer 'citizen scientist' and †Year 2010 were used as reference categories; significance categories were set as '***'$P < 0.001$, **$P < 0.01$, *$P < 0.05$.*

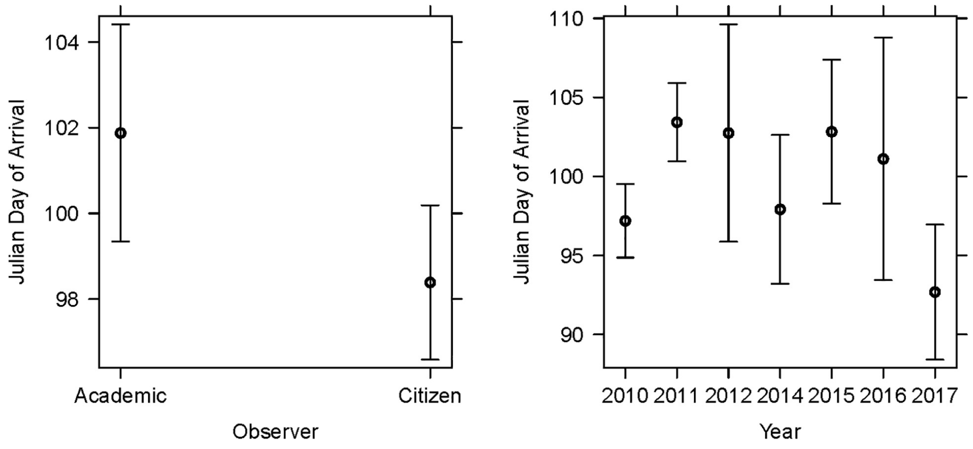

FIGURE 4 | The LMM on arrival dates featured observer category and study year as significant explanatory terms. The overall R^2c of the LMM was 0.21. Model details in **Table 1A**.

Dependency of Egg-Laying on Arrival Date

A final LMM was performed using the smaller data set of corresponding observations (n = 68) which provided arrival and egg-laying dates from the same nests and breeding seasons. Weather variables, arrival dates, SSF and year were fitted as fixed effects and nest ID as a random term (R^2LMMc = 0.85; **Table 2**). Observer category could not be included as the respective events were not necessarily reported by the same observer. While the overall significant year effect [$\chi^2_{(6,68)} = 19.06$, $P = 0.004$] had no clear direction (i.e., there was no increasing advance or delay over the course of the years, but egg-laying started earlier in some years and later in others), PP [$\chi^2_{(1,68)} = 71.65$, $P < 0.001$] and T_{max} [$\chi^2_{(1,68)} = 49.38$, $P < 0.001$] were both positively correlated with later egg-laying dates (**Figure 6**). Additionally, later arrival resulted overall in slightly later egg-laying [$\chi^2_{(1,68)} = 3.83$, $P = 0.050$], while there was no variation along the urban gradient [SSF $\chi^2_{(1,68)} = 0.04$, $P = 0.850$]. However, the time gap between arrival and egg-laying date (Δ Days) decreased for later arrival dates [**Figure 7**; $F_{(1,66)} = 33.29$, $P < 0.001$, $R^2 = 0.33$, estimate = -0.59 ± 0.10 SE], which means egg-laying started relatively earlier with corresponding later arrival date. Δ Days decreased by approximately half a day per later day of arrival.

DISCUSSION

Our results suggest that the breeding phenology of urban kestrels in Vienna is highly affected by weather variables. Precipitation was the most informative variable for predicting egg-laying dates, within a time window starting before the arrival at the nest site and ending 3 weeks before egg-laying. Additionally, the model on egg-laying dates identified observer category as a significant predictor and indicated earlier egg-laying in more natural areas, while also revealing strong inter-annual variation. Finally, the time gap between arrival and egg-laying was shorter in breeding pairs that arrived later at their nest sites, perhaps to take advantage of potentially favorable conditions at the wintering grounds while avoiding egg-laying delay and the associated declines in breeding productivity with later onset of breeding known from the urban breeding habitat.

Weather Shapes Breeding Phenology

In general, the reproduction of birds is influenced by temperature and precipitation (Crick and Sparks, 1999), but only a more detailed identification of critical time windows allows us to predict potential impacts of climate change (van de Pol and Cockburn, 2011). Our associative approach on the critical time windows (Brommer et al., 2008) revealed that the most informative time windows spanned from roughly 11–3 weeks before egg-laying for precipitation and 5 to 3.5 weeks for temperature. The mechanistic pathways behind the influence of precipitation and temperature on egg-laying include direct effects on energetic demands of females and gonadal growth of both sexes, and indirect effects on food sources (Dunn, 2004) that in turn control prey availability and ultimately hunting success. However, a previous study on the kestrel population of Vienna verified a stronger connection between breeding performance and weather parameters than between breeding performance and diet composition (Kreiderits et al., 2016). Nevertheless, prey availability could not be assessed for the entire long-term study period used in this current investigation.

Our findings emphasize the role of precipitation as cue for clutch initiation, but surprisingly, the critical time windows started way before the peak of arrivals at the nest site (after migration) 4–3 weeks before egg-laying. We consider two potential reasons. Firstly, kestrels are short-distance migrants (Village, 1990), although the detailed wintering grounds and migration routes of the Viennese kestrel population remain unknown. It is therefore possible, but at this stage speculative, that they experience similar macroclimates at their wintering grounds and breeding sites. In Europe, precipitation and temperature are closely related to the North Atlantic Oscillation in terms of long-term trends and in the frequency of

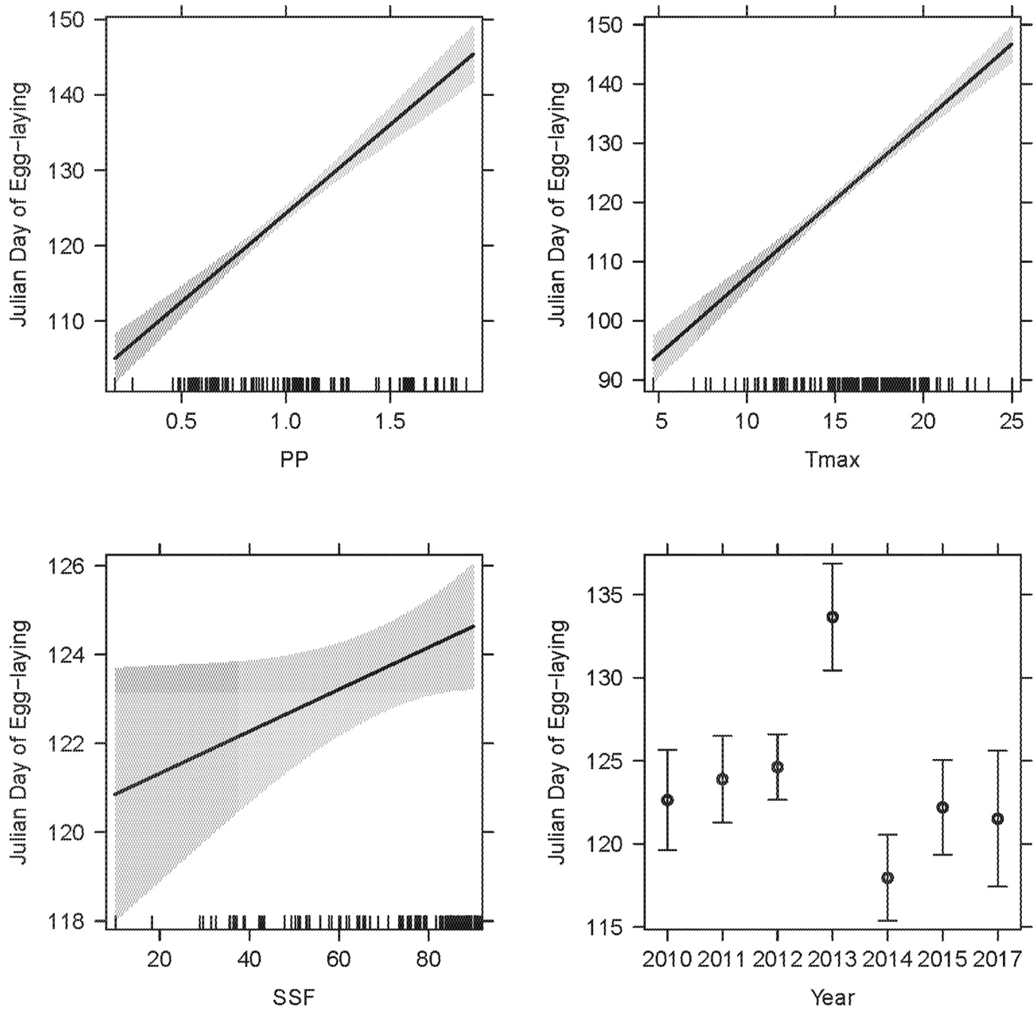

FIGURE 5 | The LMM on egg-laying dates featured two weather variables (PP, T_{max}), year, SSF and observer category (not depicted) as significant explanatory terms. The overall R^2LMMc was 0.77. Model details in **Table 1B**.

extreme weather events (Hurrell, 1995; Scaife et al., 2008). Both local weather and winter North Atlantic Oscillation can explain variation in egg-laying dates of Mediterranean kestrels (Costantini et al., 2010a). However, in contrast to our population the one in Rome only shows facultative winter dispersion (Costantini et al., 2010b), a phenomenon that also seems to have increased in frequency in Vienna (pers. obs.) but comprehensive data on this issue are currently missing. Secondly, previous findings have shown that dry and mild winters have positive effects on the proportion of mammals in the kestrel's diet (Kreiderits et al., 2016) – which is their main prey (Village, 1990). In consequence, the weather before breeding might have direct and indirect effects on phenology.

Interestingly, the weather conditions closer to egg-laying appeared to be less influential, as the critical time windows ended 3 weeks before egg-laying, indicating a time gap between cue and response. The time window did not overlap with the actual development of the eggs within the body, which supposedly starts 9 days before laying of the first egg (Meijer et al., 1989). Lag times are generally considered disadvantageous, as they enhance the probability of mismatches between environmental optimum and breeding effort, but time scales are dependent on the environmental variability (Padilla and Adolph, 1996). So far, negative consequences of such mismatches on the reproductive performance have been mainly reported for birds depending on a close match in timing of egg laying and the biomass peak of caterpillars used as food for the nestlings [e.g., great tits *Parus major* (Charmantier et al., 2008); European pied flycatcher *Ficedula hypoleuca* (Visser et al., 2006, 2012)]. However, as vertebrate prey does not show such a pronounced seasonal biomass peak as found in caterpillars, it may be easier for kestrels to compensate for late territory acquisition, particularly when they are capable of reducing the time gap until egg-laying.

Although both climatic variables featured significantly into our models, we assume precipitation to be more informative than

TABLE 2 | LMM on egg-laying dates from corresponding observations (2010–2012, 2014–2015, and 2017–2018) exploring the effects of arrival date, precipitation (PP, mean from 21 to 79 days before egg-laying), maximum temperature (T_{max}, mean from 20 to 40 days before egg-laying), Soil Seal Factor (SSF) and year.

	Estimate	***SE***	χ^2	***P***	**Sign.**	**R^2 LMMc**
Egg-laying date ∼ arrival date + PP + T_{max} + SSF + year + (1 | nest ID)						0.85
Arrival date	0.11	0.06	3.83	0.050	*	
PP	20.67	2.44	71.65	<0.001	***	
T_{max}	2.43	0.35	49.38	<0.001	***	
SSF	0.01	0.03	0.04	0.850	–	
Year†	1.03	2.45	19.06	0.004	**	
2011	5.12	3.79				
2012	−7.27	2.65				
2014	−2.42	2.58				
2015	−4.53	2.47				
2017	1.21	6.16				
2018	0.11	0.06				
Intercept	52.99	6.14	74.56	<0.001	***	

*We assessed the significance of explanatory terms using their partial (Type III) significance values (χ^2-tests). †Year 2010 was used as a reference category; significance categories were set as ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.*

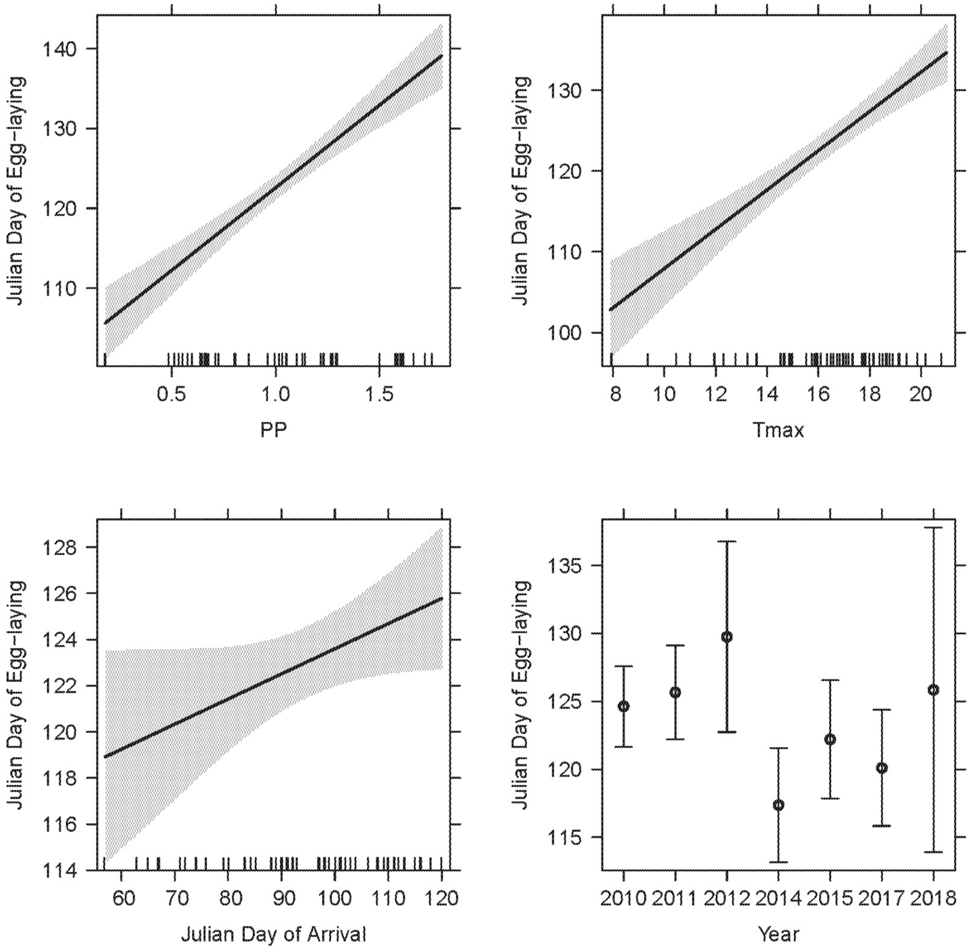

FIGURE 6 | The LMM on egg-laying dates from corresponding observations featured two weather variables (PP, T_{max}), year and arrival date as significant explanatory terms. SSF (not depicted) was not significant. The overall R^2c of the LMM was 0.85. Model details in **Table 2**.

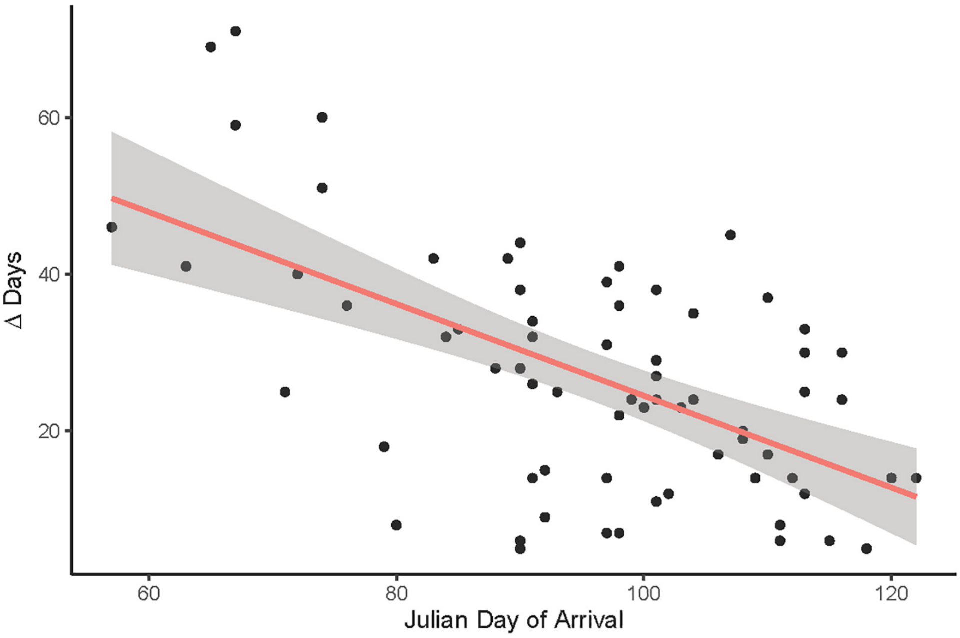

FIGURE 7 | The time gap between arrival and egg-laying date (Δ Days) shortens for later arrival dates when pooling corresponding arrival and egg-laying observations from all years (n = 68). R^2 = 0.28, P < 0.001.

maximum daily temperature. Despite the inter-annual variation of weather variables and egg-laying dates, it is inevitable that daily maximum temperatures will increase with advancing time of the year. Hence, we argue that earlier breeders will naturally face colder temperatures within the given time window rather than higher temperatures postponing egg-laying as implied by our findings. Precipitation on the other hand showed less seasonal trends. Higher amounts of rainfall during the critical time window delayed egg-laying, which supports previous studies on kestrels (Carrillo and González-Dávila, 2009; Costantini et al., 2010a; Kreiderits et al., 2016). This delay might be caused by prey availability, as higher rainfall reduces both prey activity (Brown, 1956) and the hunting activity of kestrels (Rijnsdorp et al., 1981). Higher food availability is generally known to advance the egg-laying date, as supplementary fed kestrels lay their eggs earlier than their conspecifics without supplementary food (Aparicio, 1994; Aparicio and Bonal, 2002). Furthermore, in kestrels the males provide supplementary food to the females long before egg laying during the courtship period (Village, 1990). When this supplementary food may be important for the females to achieve a minimum body condition required for initiating egg production, then negative consequences of rainfall may already effect the egg laying date weeks in advance.

Compensation of Later Arrival by Shortening of Courtship Period

Another significant predictor for egg-laying date was the arrival date itself, but kestrels which arrive later at the nest site do not necessarily delay their egg-laying by the same amount of time. The courtship period, defined as the time from arrival until egg-laying, decreased dramatically with later arrival (half a day decrease per later day of arrival). This might be a strategy to mitigate expected fitness costs of the late arrival for the offspring (Daan et al., 1989), while reducing fitness costs for the parents. Meaning, urban core areas might be attractive as breeding territories due to a high nest site availability but also are characterized by a low food availability (Sumasgutner et al., 2014a,b) known to lead to impaired health (Sumasgutner et al., 2018) and lower fledging success (Sumasgutner et al., 2014a).

Because of this challenge the parents might benefit from extending their time in probably more rural wintering habitat to gain a better body condition, which in turn positively influences breeding productivity (Drent and Daan, 1980). Indeed, experimentally supplemented food (Dijkstra et al., 1982; Korpimäki and Wiehn, 1998) and superior hunting skills of the male (Masman et al., 1986) are known to lead to considerably earlier laying dates in kestrels. However, in several raptor species including kestrels, egg-laying date is also influenced by individual age and breeding experience (Forslund and Pärt, 1995; Daunt et al., 1999; Sumasgutner et al., 2014c, 2019a), intraspecific competition for territories (e.g., Sergio et al., 2007) or social cues provided by conspecifics (Danchin et al., 2004; Sumasgutner et al., 2014c). Ultimately, it remains difficult to assess the effect of shortened courtship periods after later arrival in an overall lower quality breeding habitat without including information on the body condition of breeding adults, individual age and breeding experience, migration distances and quality of the wintering habitats of the observed individuals. Such data are not yet available for the study population.

Observer Category Matters

The underlying monitoring program is designed as a citizen science project, so the data is provided by academic and citizen scientists contributing their observations. We found a significant relationship between arrival and egg-laying dates and observer category. Citizen scientists observed the arrivals of kestrels on average 1 week earlier than academic scientists. This is very logical for methodological reasons. Firstly, most citizen scientists monitor a nest site close to their work place or home, which allow daily nest checks. Secondly, offices and homes often offer a direct view into the nest sites, a clear advantage over working from street level. Thirdly, the systematic monitoring by academic scientists was initiated only once the first reports of citizen scientists accumulated.

In contrast, mean egg-laying dates only differed by less than 1.5 days between citizen scientists and academic scientists. However, only a few citizen scientists reported egg-laying dates, usually those with a direct view into the nest content such as a planter box on the windowsill. The academic scientists on the other hand back-dated most egg-laying dates when assessing nestlings' development during banding (Kostrzewa and Kostrzewa, 1987, 1993; Village, 1990). Hence, we see a strong methodological constraint to this result as citizen scientists simply have limited options to assess egg-laying dates, but we included the variable in all analyses to control for such possible effects.

We conclude that citizen scientists add valuable data to this project. Citizen science is known to decidedly increase the scale of ecological field surveys by broadening the sample size and geographical extent and is highly valued as complementary approach in synergy with research by academic scientists (Dickinson et al., 2010; Miller-Rushing et al., 2012; Chandler et al., 2017). However, due to the above-mentioned factors, observer category should be considered when analyzing data on arrival or egg-laying dates to control for variation linked to the methodology.

No Effect of Urbanization on Arrival but Indicative for Egg-Laying Dates

Interestingly, with this larger data set, we could not confirm a previous finding of earlier arrival dates in more urbanized areas (effect of the Soil Seal Factor), even though the direction remained the same. The original study was limited to the years 2010–2012, with a marginally non-significant result (Sumasgutner et al., 2014a). With this longer data-set, urbanization had a marginally significant effect on egg-laying dates, in a way that later egg-laying was observed in more urbanized areas. This is remarkable, as urbanization usually correlates positively with earlier egg-laying dates in several passerine bird species (Chamberlain et al., 2009; Møller et al., 2015; de Jong et al., 2018) and also some raptor species [Cooper's hawks *Accipiter cooperi* (Boal and Mannan, 1999); Crested goshawks *Accipiter trivirgatus* (Lin et al., 2015); Peregrine falcons *Falco peregrinus* (Sumasgutner et al., 2020); and Tawny owls *Strix aluco* (Solonen, 2014)]. This phenological shift is often attributed to the urban heat-island effect (Oke, 1982; Arnfield, 2003; Streutker, 2003), which is likely to exist in Vienna. Higher ambient temperatures in urban areas are caused by the heat-absorbing properties of urban structures (i.e., sealed surfaces) together with the scattering effects of air pollution, which traps radiated heat within the atmosphere of the city. The average temperature difference between cities and the surrounding countryside is usually around 2.9°C (Imhoff et al., 2010). In our study we accessed detailed weather data for the entire length of the study period from one weather station and were thus not able to obtain finer scale data per territory which would be needed to shed light on possible local differences.

The expected shift in breeding phenology appears less consistently in urban raptors, as two studies even reported a weak (non-significant) evidence for a later onset of breeding at urban sites [in Kettel et al., 2018: Bald eagles *Haliaeetus leucocephalus* (Millsap et al., 2004); and Burrowing owls *Athene cunicularia* (Conway et al., 2006)]. Furthermore, a comparative study on Eurasian kestrels in Israel also found pairs breeding on average 2 and 8 days earlier in more rural environments, compared to towns and cities (Charter et al., 2007). Overall, raptors respond less consistently to urbanization (Marzluff, 2001), and all reported differences in an urban raptor review (Kettel et al., 2018) were based on a one by one urban-rural comparison, while reviewed studies using an urban gradient approach did not find any effect of urban land cover on the onset of egg-laying [in Barn owls *Tyto alba* (Frey et al., 2011), and American kestrels *Falco sparverius* (Strasser and Heath, 2013); but see Sumasgutner et al., 2020].

CONCLUSION

We need to acquire knowledge on the wintering grounds of the studied kestrel population to gain a deeper understanding of arrival dates and factors which might ultimately shape breeding phenology. For example, the time of departure and migration speed could vary, depending on year, but also between locations where kestrels might overwinter (Lehikoinen et al., 2004) which could result in carry-over effects which would then, in turn, be visible in high inter-annual variation of arrival times which were also well pronounced in our data. Additional to unknown migration distances, we can also only speculate about local weather conditions or prey availability on the wintering grounds.

However, we gained a much better understanding on variation in egg-laying dates. Most evidence thus far focuses on weather conditions experienced close to the egg-laying date itself or uses monthly means (Costantini et al., 2010a), which might limit the explained variation compared to the sliding window approach applied here (Brommer et al., 2008; Williams et al., 2015). We found that, beside precipitation and temperature, the degree of urbanization was another potentially relevant factor, with kestrels breeding in more natural areas laying their clutches earlier than their conspecifics in urban core areas. However, the effect size of this result was rather small, and so we suggest a future investigation on nesting microclimate (see for instance Catry et al., 2011 on temperature nest type correlations which could also play an important role in our system).

When testing the effect of arrival date on egg-laying dates we also found a shortened courtship period in later arriving breeding pairs, resulting in relatively earlier egg-laying. Later clutches generally face higher fitness costs and are less likely to produce offspring which recruits into the breeding population (Perrins, 1970). The shortening of the courtship period might be a strategy to mitigate the negative effects of later broods while taking advantage of potentially favorable condition at the wintering ground. Ultimately, this would add to the body of evidence that kestrels are able to adapt physiologically and behaviorally to urban environments, despite our concern about cities creating an ecological trap for the species (Sumasgutner et al., 2014a). Considering their potential ability to use environmental cues for the fine-tuning of breeding phenology to the environmental optimum, European kestrels might be able to adapt to the human-induced climate change in the long-run.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

The animal study was reviewed and approved by Environmental Protection Bureau of Vienna (MA22/1263/2010/3) and the Ministry for Science and Research (BM.WF ± 66.006/0021-II/3b/2013). All data collection was conducted in strict accordance with current Austrian law and followed the Weatherall Report and the guidelines for the treatment of animals in behavioral research and teaching (ASAB, 2018).

AUTHOR CONTRIBUTIONS

The idea for this study originally came from PS, CS, and KH. The Viennese kestrel project and all citizen science involvement were coordinated by PS and AG. Environmental data was collected by PS and KH. Help by others is accordingly acknowledged. The statistical analyses were performed by KH and CS. The manuscript was prepared by KH and PS with edits provided by CS. All authors contributed to the article and the submitted version was approved by KH, CS, and PS.

DEDICATION

This article is dedicated to Anita Gamauf (*1962–2018†).

FUNDING

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00247/full#supplementary-material

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Incubation in a Temperate Passerine: Do Environmental Conditions Affect Incubation Period Duration and Hatching Success?

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The timing of breeding often has a profound influence on the reproductive success of birds living in seasonal environments with rapidly changing nestling food availability. Timing is typically investigated with reference to lay dates, but it is the time of hatching that determines the ambient conditions and food availability that nestlings experience. Thus, in addition to lay date, phenological studies may also have to take account of variation in the length of the incubation period, which is likely to depend on both environmental conditions and parental traits. The primary aim of this study was to use a 24-year dataset to investigate the abiotic and biotic factors influencing variation in incubation duration in long-tailed tits (*Aegithalos caudatus*), a species in which incubation duration varies substantially (range: 12–26 days). We found support for our predictions that drier conditions, later breeding attempts and larger clutches were associated with shorter incubation periods. Larger clutches were also more resilient to increases in incubation duration associated with wet conditions. Surprisingly, warmer ambient conditions were associated with longer incubation periods. Secondly, we assessed the consequences of variation in the length of incubation periods for the risk of nest predation and the hatching success of surviving clutches. We show that longer incubation periods are likely to be costly due to increased exposure to nest predators. In contrast, we found only marginal effects of environmental conditions or incubation duration on hatching success, implying that wet conditions cause slower embryo growth and hence longer incubation periods, rather than causing embryo fatality. We suggest that long-tailed tits' nests and parental behavior protect eggs from mortality arising directly from adverse weather conditions.

Keywords: climate, incubation length, microclimate, parental investment, thermal environment, seasonal variation

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INTRODUCTION

Reproductive success of birds is often dependent upon timing of breeding (Daan et al., 1997; Houston and McNamara, 1999), with individuals that breed earlier in the season typically having higher fitness (Perrins, 1970; Both, 2010). For many bird species living in seasonal environments, it is critical for reproduction to be timed to match temporally ephemeral food resources, with hatching expected to coincide with the peak of food abundance (Perrins, 1970; Monros et al., 1998; Naef-Daenzer et al., 2004; Simmonds et al., 2017). A large number of studies have focused on variation in clutch initiation date (e.g., Visser et al., 1998; Charmantier et al., 2008; Schaper et al., 2012), but other mechanisms for altering the timing of hatching exist. Females may adjust the length of the egg-laying period by altering clutch size, or by increasing the intervals between laying (Haftorn, 1981; Nilsson and Svensson, 1993; Simmonds et al., 2017). Alternatively, the length of the incubation period could be adjusted by starting incubation prior to clutch completion or by delaying the start of incubation (Haftorn, 1981; García-Navas and Sanz, 2011; Nord and Nilsson, 2011; Álvarez and Barba, 2014; Simmonds et al., 2017), and by changing nest attentiveness once incubation has started (Martin et al., 2007; MacDonald et al., 2013; Coe et al., 2015).

Incubation is typically an energy- and time-consuming component of avian reproduction (Tatner and Bryant, 1993; Williams, 1996; DuRant et al., 2013a; Nord and Williams, 2015) due to the relatively high temperatures (34–40°C) at which eggs must be maintained to ensure optimal embryonic development (Webb, 1987; DuRant et al., 2013b). Investment in incubation reduces the energy and time available for parents to spend on self-maintenance (Stearns, 1989; Reznick et al., 2000; Zera and Harshman, 2001), especially in species in which one parent is solely responsible for incubation (Deeming, 2002). Consequently, incubation can reduce parental body condition (Tombre and Erikstad, 1996; Hanssen et al., 2005) and immune function (Knowles et al., 2009), thereby lowering fitness by reducing adult survival (Visser and Lessells, 2001) and future reproductive success (Reid et al., 2000a; Hanssen et al., 2005).

The ability of incubating parents to maintain suitable conditions for embryo development may also be affected by environmental factors. For example, lower ambient temperatures can alter the nest microclimate, causing eggs to cool at a faster rate and reach lower temperatures when left unattended (Reid et al., 2000b). This means that an incubating parent must expend more energy re-heating cooled eggs and maintaining eggs at the optimal temperature (Jarvinen, 1993; Sheaffer and Malecki, 1996; Skinner et al., 1998). Eggs that experience low or fluctuating temperatures not only suffer from reduced hatching success, but also from slower embryonic growth (Olson et al., 2006), production of poorer quality offspring (Nord and Nilsson, 2011; DuRant et al., 2013a) and reduced long-term survival of offspring (Berntsen and Bech, 2016). In addition, heavy rain also leads to reduced hatching success and nest failure in some passerine species (Wesołowski et al., 2002; Martin et al., 2017), an effect that has been attributed to enhanced heat loss from eggs via increased conductance and reduced insulating properties of damp nest materials (Reid et al., 2002; Hilton et al., 2004; Heenan, 2013). Thus adverse weather conditions can have profound consequences for both the length of the incubation period and hatching success.

However, there are ways in which negative environmental impacts may be mitigated, such as by building well-insulated nests (Deeming and Gray, 2016), or by increasing incubation attendance when temperatures are lower (Conway and Martin, 2000; Amininasab et al., 2016). In addition, clutches of different sizes have different thermal properties; the thermal inertia hypothesis predicting that larger clutches should cool more slowly, while also taking longer to re-heat (Reid et al., 2000b; Cooper, 2005). This hypothesis is supported by the observation that large clutches in tree swallows *Tachycineta bicolor* have shorter incubation periods (Ardia et al., 2006), although most studies have found no effect of clutch size on the length of the incubation period (Székely et al., 1994; Siikamiiki, 1995; Sandercock, 1997; Reid et al., 2000a; Wiebe and Martin, 2000), suggesting that, in general, the thermal properties of the clutch do not have a significant effect on the duration of the incubation period.

The extent to which females can mitigate the negative impacts of climate may depend on their age (e.g., female age was positively correlated with nest temperature in blue tits *Cyanistes caeruleus*; Amininasab et al., 2016), or their own quality or body condition. For example, Ardia and Clotfelter (2007) found that young female tree swallows that had their feathers clipped to induce poor condition passed the costs of this on to their offspring through lower egg temperatures. Older females also suffered self-maintenance costs from this experimental treatment, but were able to maintain higher egg temperatures and produce higher quality offspring. These studies indicate that older females may be more willing to bear self-maintenance costs and not pass these on to their offspring.

We investigated the effects of timing of breeding and environmental conditions on incubation periods and hatching success in the long-tailed tit *Aegithalos caudatus*. Long-tailed tits build domed nests that require a large investment of time and energy (McGowan et al., 2004). The nest is constructed of moss and fibers bound together with spiders' silk, covered on the outside with flakes of lichen and lined with up to 2,500 feathers, with a small entrance hole (Hansell, 1996; McGowan et al., 2004). Only females incubate the eggs, spending about 65% of daylight hours on the nest, while males bring food to incubating females on average twice an hour (Hatchwell et al., 1999). Long-tailed tits are facultative cooperative breeders, but helpers assist only in the feeding of nestlings and fledglings (Gaston, 1973; Hatchwell et al., 2004) and are not present during incubation. Long-tailed tits are well suited to this study because there is much natural variation in the length of time between their last egg being laid and the hatching of their eggs, henceforth referred to as the incubation period (range: 12 to 26 days), the causes and consequences of which are unknown. Also, there is a high rate of nest predation (72%; Gullett et al., 2013; Hatchwell et al., 2013), so longer incubation periods could significantly increase the risk of nest failure.

In this study, first we used a 24-year dataset to test whether incubation period was associated with weather variables (temperature and precipitation), timing of breeding (clutch completion date and attempt number), clutch size and female age. We predicted that incubation periods would: (i) be longer in cold and wet weather conditions; (ii) decrease later in the season and in replacement nests; and (iii) that clutch size would influence incubation duration – either increasing it for larger clutches because more energy is required for incubation, or decreasing it for larger clutch sizes because eggs retain more heat during female foraging bouts, as predicted by the thermal inertia hypothesis. We also predicted: (iv) that older females would be better incubators, thus reducing incubation period duration. Secondly, we tested whether environmental conditions or incubation period duration influenced hatching success. We predicted that cooler, wetter conditions and longer incubation periods would increase hatching failure rates because they were likely to be associated with lower egg temperatures that reduce embryo viability. Finally, we calculated the daily predation risk of nests during incubation to determine the consequences of variation in the length of the incubation period for the probability of nest failure.

MATERIALS AND METHODS

Study System

Long-tailed tits were studied between 1995 and 2018 in the Rivelin Valley, Sheffield (53°23′N, 1°34′W). Each year the study site contained 25–72 pairs that had 33–114 monitored breeding attempts; c. 95% of breeders were ringed with a British Trust for Ornithology (BTO) ring and a unique combination of two color rings (under BTO license). Nestlings were ringed 11 days after hatching and unringed immigrants to the study site were captured using mist nets and ringed at the beginning of the breeding season.

Long-tailed tits are single-brooded, but breeding attempts frequently fail prior to fledging and if there is sufficient time remaining in the breeding season pairs will initiate another breeding attempt (MacColl and Hatchwell, 2002). The major reason for these failures is predation by both avian and mammalian predators (Hatchwell et al., 1999). Due to the high rate of breeding failure and to maximize the sample size for each analysis the sample sizes vary as follows. For this study, 540 breeding attempts that reached the incubation stage were monitored; of these, 372 clutches hatched and 230 broods survived until day 11 when nestlings were counted. Nests were routinely monitored every 2 days, and daily around the time of hatching, to obtain accurate reproductive parameters, i.e., first egg date, clutch size, hatching date, and either fledging or failure date. A very small percentage of nests, estimated to be <5%, are not found in each year but these undetected nesting attempts typically fail early in the breeding cycle (Sharp et al., 2008).

Measuring Incubation Period

We followed many previous studies by measuring incubation period as the number of days between clutch completion and hatching (Nilsson and Smith, 1988; Wiebe and Martin, 2000; Martin, 2002; Martin et al., 2007; Rohwer et al., 2015; Bueno-Enciso et al., 2017). Our procedure for determining incubation period was as follows. The date the first egg of each clutch was laid (hereafter referred to as first egg date) was recorded as a date within the year, where 1st March is set as day 1. Long-tailed tits lay a single egg per day, around dawn, and we counted the number of eggs in a clutch on or around the day the 12th egg would have been laid; this is the largest clutch size recorded in the 26 years of our study. From this we calculated the date of clutch completion. The assumption that females commenced incubation only after clutch completion is justified by observations that females do not start incubation until their last egg was laid (Glen, 1985; B. J. Hatchwell personal observation) and also by the observation that hatching is synchronous. We confirmed that short incubation periods were not a consequence of incubation starting prior to clutch completion by examining whether nestling size hierarchies were greater in broods with shorter incubation periods, which would be the expected result of early incubation and hence asynchronous hatching (Slagsvold et al., 1995; Stenning, 2008). We calculated asynchrony as the mass of the heaviest nestling in a brood minus the mass of the lightest nestling in a brood, divided by the mean mass of the brood (Kluen et al., 2011). There was no significant difference in the degree of asynchrony of broods in the lower (range: 12 to 15 days) and upper (range: 17 to 26 days) quartiles of incubation period ($F_{(1,73)} = 0.03$, $P = 0.20$). Hatching date was recorded by checking nests at daily intervals from the earliest expected date of hatching; given that eggs could hatch shortly after one nest-check and hence up to 1 day before being checked again, hatch dates were accurate to within 1 day.

Our measure of incubation duration is thus dominated by the period during which females incubated eggs, but it also includes any delay in the start of incubation after laying the final egg. Such delays do sometimes occur in long-tailed tits, but it was not logistically feasible to routinely record the date on which females started incubation for all nests. However, we were able to estimate how frequent a delayed start to incubation was by noting whether the eggs were warm to the touch when eggs were counted 12 (n = 103), 11 (n = 35) or 10 (n = 22) days after the first egg date. For this sub-sample of breeding attempts, 8.1% (n = 160) of females had not begun incubation when the nest was checked. Of the remaining 147 breeding attempts we calculated the maximum potential delay in starting incubation as the difference between the day the last egg was laid and the day the eggs were counted. We then compared this to the delay in hatching (number of days beyond the shortest incubation in our study) and found that 87.1% of them had a greater delay in hatching than could be accounted for by simply delaying the start of incubation. This indicates that while some of the longer incubation periods may be due to delays in the start of incubation, most are indeed due to active incubation by females lasting longer. Moreover, given that any delay in the start of incubation may be attributable to poor weather (Rowe and Weatherhead, 2009), any effect would be consistent with our hypothesis that adverse environmental conditions prolong the incubation period and extend the period of predation risk.

To account for the considerable inter-annual variation in the timing of breeding caused by variable early spring temperatures (Gullett et al., 2013), we calculated relative first egg date and relative clutch completion date. For each breeding attempt, we calculated the number of days between the dates of these events for a given nest and the earliest first egg and earliest incubation start dates recorded in that year. Only breeding attempts for which first egg date, clutch size and hatch date information was available were used in analyses, leaving 372 breeding attempts by 289 females remaining in our dataset. The incubation period for these breeding attempts ranged from 12 to 26 days (mean ± SD = 16.4 days ± 1.56, median = 16 days). The dataset contained two outliers (incubation durations of 23 and 26 days) and analyses were conducted with and without outliers. We report analyses including outliers in the main text, but the results from analyses with and without outliers are reported in **Supplementary Tables S1 and S2**, respectively.

Measuring Hatching Success

Brood size when nestlings were 11 days old was used to estimate the number of eggs that had successfully hatched. Long-tailed tits have a low nestling mortality rate due to starvation between hatching and day 11 (2.3% of nestlings; Hatchwell et al., 2004), and partial nest predation is also rare. Thus, it is very likely that a small brood size on day 11 is due to hatching failure rather than nestling mortality; and this was confirmed in the majority of cases by the presence of unhatched but intact eggs in the nest on day 11. Hatching success was variable (range = 12.5–100%) but high on average (mean = 81.8%; median = 88.9%). Note that since some broods were completely depredated between hatching and day 11 our sample size for this analysis was smaller than for the incubation period study ($n = 230$).

Weather Data

Weather data for 1995–2018 were obtained from Weston Park Meteorological Station (Museums Sheffield, 2019), located 5 km east of the center of the study site and at a similar elevation (131 m above sea level compared with mean field site altitude of 168 m). Temperatures at the weather station are significantly positively correlated with those recorded at the field site (Gullett et al., 2014), and were used because on-site temperature data were not available for all years. Given strong spatial autocorrelation in precipitation patterns (Burton et al., 2013) the close proximity of the weather station to the study site also means that the difference in precipitation between the weather station and field site is minor (Gullett et al., 2014), although we have no direct measurements of precipitation from the field site to compare to the weather station data.

We calculated mean daily temperature, mean daily minimum temperature, mean daily maximum temperature, mean daily rainfall, and the proportion of rainy days during the incubation period of each nest ($n = 372$). Initially, we defined the proportion of rainy days in three ways: (i) the proportion of days with any rain (>0 mm), (ii) the proportion of days with >0.35 mm of rain (which excludes the least rainy 10% of days), and (iii) the proportion of days with >3 mm of rain (which excludes the least rainy 75% of days). However, mean daily rainfall during the incubation period, and all three measures of the proportion of rainy days were closely positively correlated (Pearson's correlation: $r \geq 0.78$, df = 370, $P < 0.001$ in all cases). Similarly, minimum and maximum temperatures were highly positively correlated with mean temperature (Pearson's correlation: $r \geq 0.87$, df = 370, $P < 0.001$ in both cases). Therefore, we used only the mean temperature and the proportion of rainy days (>0 mm) in our main statistical models. These variables were significantly negatively correlated (Pearson's correlation: $r = -0.47$, df = 370, $P < 0.001$), but this collinearity was well within the threshold to which information theoretic approaches are robust (VIF < 2; Freckleton, 2011). The proportion of rainy days variable was used instead of mean rainfall because it provides a better indicator of daily rainfall patterns, which we considered more likely to affect the nest's insulation quality throughout the incubation period than total rainfall. However, the analysis was also conducted using mean daily maximum temperature, mean daily minimum temperature, mean daily rainfall and the proportion of days with >3 mm of rain and the results were qualitatively similar (**Supplementary Tables S3–S5**).

Statistical Analysis

All statistical analyses were conducted in R 3.3.1 (R Core Team, 2016). We used an information theoretic approach to model selection and constructed all possible models given our predictor variables but retained year (as a random effect) in all models. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to compare model fit (Burnham and Anderson, 2002). We report the results of all models within 2 AIC_c points of the model with the lowest AIC_c value. This methodology allows us to compare all possible models and identify competing models that could equally well describe our data. To test how well the models fit our data, we used the MuMIn package (Barton, 2018) to calculate marginal and conditional pseudo-R^2 using the methods described by Nakagawa and Schielzeth (2013). The model-averaged estimates (mean and 95% confidence intervals) were also calculated. Effects were considered statistically significant when the 95% confidence intervals for a parameter estimate did not span zero (Burnham and Anderson, 2002).

Factors Affecting Incubation Period

To investigate factors affecting incubation period we constructed restricted maximum likelihood linear mixed models using the lmer function in the *lme4* package (Bates et al., 2015). Incubation period was modeled as a function of the proportion of rainy days, mean daily temperature, relative incubation start date, clutch size, attempt (whether it was a first or replacement nest as a binary factor) and female age (in years from ringing as a nestling for philopatric recruits and assuming that immigrant recruits were yearlings when first ringed (McGowan et al., 2003); year was included as a random factor. We also included six interactions, although only one interaction was ever present in any single model. The six interactions were between mean daily temperature and the proportion of rainy days, mean daily temperature and relative incubation start date, mean daily temperature and clutch size, proportion of rainy days and incubation period start date, proportion of rainy days and clutch size, and clutch size and incubation period start date. All continuous variables were scaled and centered. Female identity was not included in the models because 77.7% of the data points came from unique females and no single female contributed more than 1.36% of the data to the analysis. In addition, we separately investigated the repeatability of incubation period in females using the rptR package (Nakagawa and Schielzeth, 2010) and found that it was not repeatable (R ± SE = 0.00 ± 0.03, $P = 1.00$). Likewise, neither lay date (R ± SE = 0.02 ± 0.07, $P = 0.41$)

nor clutch size (R ± SE = 0 ± 0.03, $P = 1$) were significantly repeatable for females.

Factors Affecting Hatching Success

We built generalized linear mixed-effects models with a binomial error structure and logit link of hatching success using the glmer function in the *lme4* package (Bates et al., 2015). Hatching success was modeled as a function of incubation period, proportion of rainy days, mean daily temperature, incubation period start date, clutch size, attempt and female age (defined as above), including year as a random factor. In addition, we included the same six interactions as in the duration of incubation period models. All continuous variables were scaled and centered. Again, female identity was not used as a random factor given the high percentage of unique individuals in the dataset (81.1%).

Analysis of Predation During the Incubation Period

To assess quantitatively how variation in incubation period affected predation risk we used the model of incubation period to predict how focal predictors, such as relative incubation start date, changed the length of the incubation period and then used the daily nest predation rate to infer predicted changes in likelihood of nest predation in a typical year. This approach assumes that predation risk is uniform through time and space so that the probability of predation is purely a function of the time at risk. We calculated the daily nest predation rate during the incubation period using the Mayfield (1975) method. This method calculated the daily predation risk facing a nest by taking the total number of nests predated during the incubation period and dividing by the total number of active nest days during the incubation period for all nests. This estimate is based on 540 nests where clutches were completed and incubation started, of which 27.4% were depredated during incubation.

RESULTS

Factors Affecting Incubation Period

An information theoretic approach to modeling incubation period identified three well-supported models (**Supplementary Table S1**). These models explained a moderate amount of variation with the random effect of year explaining approximately half of this variation (conditional R^2 = 34.5%; marginal R^2 = 17.2%). The relative incubation period start date was present in all models, with pairs breeding later in the year having shorter incubation periods (**Table 1** and **Figure 1A**). Weather variables were also important because they were present in all four top models, with incubation periods increasing at higher temperatures (**Table 1** and **Figure 1B**) and as the proportion of rainy days increased (**Table 1** and **Figure 1C**). Larger clutch sizes were associated with shorter incubation periods (**Table 1** and **Figure 1D**). All of the top models also contained an interaction term between clutch size and proportion of rainy days, which indicated that the effect of increased rainfall on incubation period was lessened by having a larger clutch (**Figure 1C**). Breeding attempt and female age were each present in two of the four top models (**Supplementary Table S1**), suggesting that the incubation period was shorter for replacement nests and younger females, but the confidence intervals for these effects' parameter estimates overlapped zero suggesting that effects were negligible (**Table 1**).

Factors Affecting Hatching Success

Three models were retained in the top subset (**Supplementary Table S6**), although these models explained only a small amount of variation in hatching success (conditional R^2 = 7.2%; marginal R^2 = 4.9%). Longer incubation periods had a negative effect on hatching success (**Table 2** and **Figure 2A**). Greater hatching success was also associated with larger clutch sizes (**Figure 2B**), younger females (**Figure 2C**) and first breeding attempts (**Table 2**), all of which were present in each of the top set of models. Lower mean temperatures and more rainy days were associated with greater hatching success, although only in one of the three models (**Supplementary Table S6**) and the confidence intervals for these effects' parameter estimates overlapped zero indicating that their effects were negligible (**Table 2**).

Effects of Incubation Period on Nest Predation Risk

Through a typical breeding season, the incubation period was predicted to decrease from 17.0 to 14.1 days (**Figure 1a**). Given a Mayfield daily nest predation rate during incubation of 0.02 this reduction in incubation period equates to the probability of predation reducing from 0.34 to 0.28 (i.e., an 18% reduction in predation). For the observed range of mean temperatures during incubation from 5.5 to 13.9°C, the models predict a change in the duration of the incubation period from 15.5 to 16.9 days (**Figure 1B**), which represents a change in predation risk probability from 0.31 to 0.34 (i.e., a 10% increase in predation). Similarly, the proportion of rainy days experienced during the

TABLE 1 | The effects of clutch size, relative incubation start date, mean temperature, proportion of rainy days, female age, attempt and the interaction between clutch size and the proportion of rainy days on the duration of the incubation period in long-tailed tits.

Fixed effects	**Slope ± 1 SE**	**95% Confidence intervals**
Intercept	16.35 ± 0.16	–
Clutch size	**−0.49 ± 0.08**	**−0.63; −0.34**
Relative incubation start date	**−0.59 ± 0.12**	**−0.83; −0.36**
Mean temperature	**0.30 ± 0.13**	**0.03; 0.56**
Proportion of rainy days	**0.26 ± 0.11**	**0.04; 0.48**
Clutch size × proportion of rainy days	**−0.21 ± 0.08**	**−0.36; −0.06**
Female age	0.02 ± 0.05	−0.08; 0.12
Attempt	−0.04 ± 0.13	−0.29; 0.21
Random effect	**Variance ± 1 SE**	
Year	0.47 ± 0.68	–

Shown are model-averaged parameter estimates and 95% confidence intervals for each fixed effect, and variance for the random effect from the three best fitting models. Confidence intervals that do not overlap zero are indicated in bold. The model-averaged $R^2_{LMM(m)}$ *and* $R^2_{LMM(c)}$ *were 17.4 and 35.1%, respectively.*

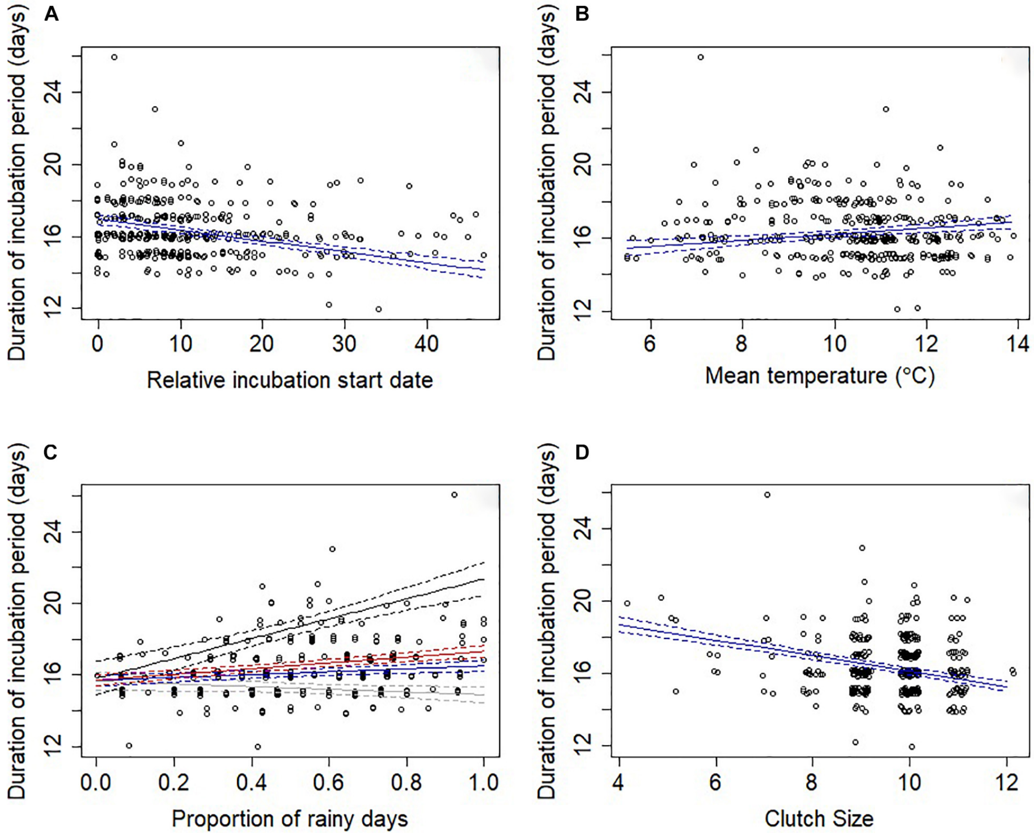

FIGURE 1 | Duration of the incubation period (days) in relation to **(A)** relative incubation start date, **(B)** mean temperature, **(C)** proportion of rainy days and **(D)** clutch size. Points have been offset so that overlapping points can be better seen. The solid lines indicate the predicted values from model-averaged parameters and dashed lines indicate the standard error. In **(C)** due to an interaction between proportion of rainy days and clutch size lines represent the model-averaged parameters when the clutch size was set to the lower quartile value (nine eggs; blue), to the upper quartile value (10 eggs; red), to the minimum value (four eggs; black) and to the maximum value (12 eggs; gray).

TABLE 2 | The effects of incubation period, clutch size, female age, attempt, mean temperature and proportion of rainy days on hatching success in long-tailed tits.

Fixed Effects	**Slope ± 1 SE**	**95% Confidence intervals**
Intercept	1.66 ± 0.09	–
Incubation period	**−0.26 ± 0.06**	**−0.39; −0.14**
Clutch size	**0.19 ± 0.07**	**0.06; 0.32**
Female age	**−0.15 ± 0.05**	**−0.26; −0.05**
Attempt	**−0.32 ± 0.15**	**−0.61; −0.03**
Mean temperature	−0.01 ± 0.04	−0.10; 0.07
Proportion of rainy days	0.01 ± 0.04	−0.06; 0.08
Random effect	**Variance ± 1 SE**	
Year	0.08 ± 0.28	–

Shown are model-averaged parameter estimates and 95% confidence intervals for each fixed effect, and variance for the random effect from the three best fitting models. Confidence intervals that do not overlap zero are indicated in bold. The model-averaged $R^2_{LMM(m)}$ *and* $R^2_{LMM(c)}$ *were 4.90 and 7.20%, respectively.*

incubation period ranged from 0 to 1, resulting in a change of incubation period from 15.7 to 16.8 days and an increase in predation risk probability from 0.31 to 0.34 (i.e., a 10% increase in predation). Clutch size ranged from 4 to 12 eggs in our sample of nests, which corresponds to a reduction in the incubation period from 18.7 to 15.3 days, under mean precipitation levels, with each additional egg resulting in the incubation period being shortened by 0.43 days and the probability of predation risk decreasing from 0.37 for 4 egg clutches to 0.31 for 12 egg clutches (i.e., a 16% reduction in predation).

DISCUSSION

Variation in the incubation period of long-tailed tits over this 24-year study was influenced by clutch size, clutch completion date, mean daily temperature, and proportion of rainy days. Incubation period was longer for smaller clutches, for breeding attempts initiated earlier in the breeding season, under warmer temperatures, and when the proportion of rainy days was higher. However, the effect of rainy days varied with clutch size because larger clutch sizes were less affected by increases in the proportion of rainy days. In addition, incubation periods were shorter in replacement nesting attempts and when females were younger, although these effects were negligible. Changes in

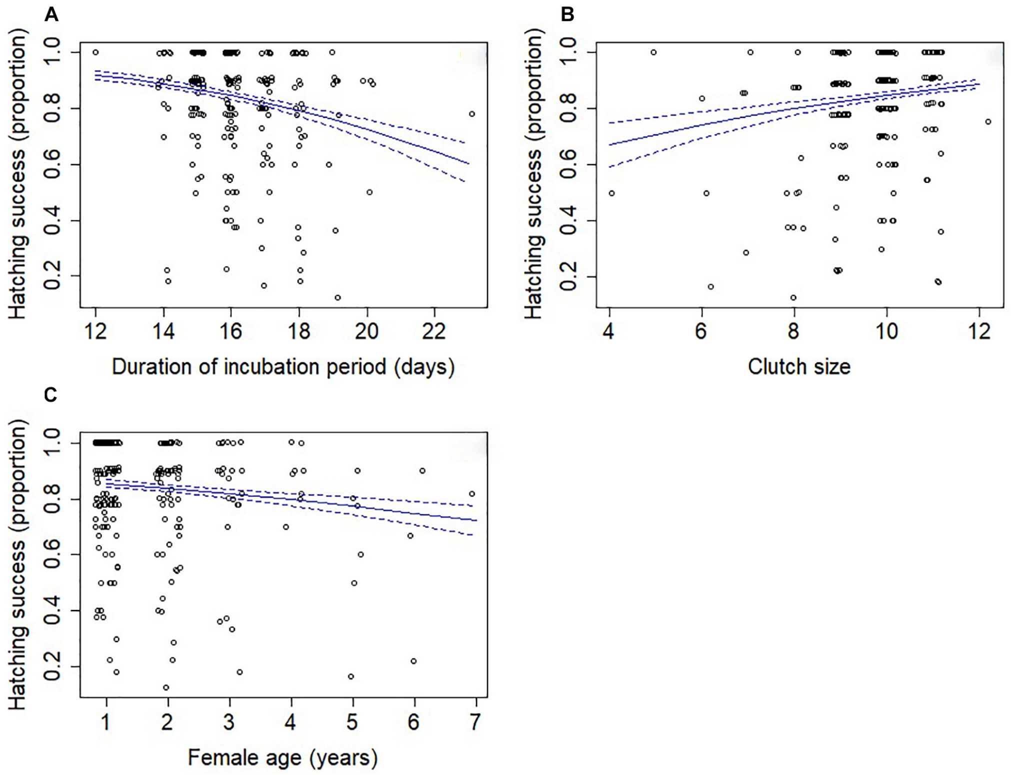

FIGURE 2 | Hatching success (proportion) in relation to **(A)** the length of the incubation period, **(B)** clutch size and **(C)** female age. Points have been offset so that overlapping points can be better seen. The solid lines indicate the predicted values from model-averaged parameters and dashed lines indicate the standard error.

incubation duration influenced the risk of nest predation during incubation with each additional day of incubation leading to predation probabilities increasing by 0.02. Modeling indicated that timing of breeding and clutch size were the most influential factors moderating nest predation risk by influencing incubation durations. Models of hatching success had limited explanatory power, but we found evidence that greater hatching success was associated with shorter incubation periods, and to a lesser extent younger females, larger clutch sizes and first breeding attempts. Mean temperature and rainfall had minimal effects on hatching success.

Shorter incubation periods toward the end of the breeding season may be advantageous by allowing nestling provisioning to occur closer to the peak abundance of insects, especially of caterpillars that constitute the major component of nestling diet at this time of year (Gullett et al., 2014). Caterpillar abundance in the Rivelin Valley typically peaks around 23 May, i.e., during the long-tailed nestling period, and nestlings in relatively early and relatively late nests are provisioned with fewer caterpillars (Gullett, 2014). Other woodland passerines that predominantly provision offspring with caterpillars also appear to alter incubation behavior in order to better match the date of caterpillar peak abundance, e.g., blue tit (Visser et al., 1998), great tit *Parus major* (Simmonds et al., 2017) and European pied flycatcher *Ficedula hypoleuca* (Both and Visser, 2005). Adult long-tailed tits have more variable diets than their nestlings and the reduction in length of the incubation period later in the season could also be due to increased abundance of other insects that enables incubating females to increase daytime nest attendance (Dewey and Kennedy, 2001; Duncan Rastogi et al., 2006) and hence reduce incubation periods (Lyon and Montgomerie, 1985; Martin, 2002; Martin et al., 2007). In addition, the rate at which males provision females on the nest during the incubation period could increase later in the breeding season leading to greater female nest attentiveness and hence shorter incubation periods, as has been shown in other passerines (Martin and Ghalambor, 1999; Eikenaar et al., 2003; Matysioková et al., 2011).

Laying a larger clutch is thought to be costly because of the additional investment in eggs and because larger broods may increase activity around the nest leading to increased predation (Skutch, 1949; Johnsgard, 1973; Perrins, 1977; Martin et al., 2000). These costs may be partially compensated for by the reduction in incubation period with larger clutches; an increase in clutch size by one egg was associated with a reduction in incubation period of approximately half a day. Ardia et al. (2006) also found that larger clutches had shorter incubation periods in tree swallows, and it has been suggested that under temperate or cold conditions it is better to have a larger clutch size as this increases thermal inertia, reducing cooling rates relative to smaller clutches (Reid et al., 2000b; Cooper, 2005). This relationship between clutch size and incubation period contrasts with experimental evidence that increased clutch sizes do not reduce incubation duration (Székely et al., 1994; Siikamiiki, 1995; Sandercock, 1997; Reid et al., 2000a; Wiebe and Martin, 2000), a discrepancy that may be due to females being unable to effectively incubate enlarged clutches in experimental treatments. Our results represent natural variation where females would presumably be able to incubate the whole clutch effectively. It may be that better quality females are able to simultaneously produce naturally larger clutches while incubating more efficiently than poorer quality females, and hence reduce the incubation period for their clutches. However, further experimental work that monitored female quality while experimentally altering clutch sizes and measuring the duration of the incubation periods would be required to test this idea.

The interaction between clutch size and the proportion of rainy days indicated that larger clutches seem to be particularly advantageous when the proportion of rainy days increased. During periods of rainfall the nest is likely to lose heat via increased conductance through damp nesting materials (Reid et al., 2002; Hilton et al., 2004; Heenan, 2013), so our result may indicate that larger clutches buffer the effects of rainfall because a smaller clutch surface area to volume ratio reduces exposure to damp nesting materials or humid and cold air. However, it is also important to consider the potential impact of weather on the behavior of incubating birds; for example, any effects of increased conductance may be confounded by females adjusting their nest attentiveness during periods of heavy rainfall and storms (MacDonald et al., 2013; Fu et al., 2017).

Contrary to our predictions, higher ambient temperatures were associated with longer incubation periods. This result is especially surprising given that previous studies have found that other species, including cavity-nesting species whose nests tend to be well insulated (Massaro et al., 2013), are likely to delay the start of incubation at colder temperatures, thus increasing the duration of incubation (great tits: Monros et al., 1998; blue tits: Kluen et al., 2011). A likely mechanism for higher temperatures increasing the duration of the incubation period is adjustment of incubation behavior under different ambient temperatures. For example, incubating females may leave the nest for shorter periods in cold conditions (Voss et al., 2006; Amininasab et al., 2016; Walters et al., 2016), so eggs remain within the optimal incubation temperature range for a greater proportion of the day. However, other studies have reported greater nest attendance when ambient temperatures are higher (Morton and Pereyra, 1985; Ardia et al., 2010; MacDonald et al., 2013; Simmonds et al., 2017), perhaps because lower costs of heating eggs and/or foraging allow females to incubate for longer before they need to forage again. Regardless of the mechanism generating the positive association we observed between temperature and incubation duration in long-tailed tits, this effect suggests that climate change will not only lead to changes in the timing of breeding (Gullett et al., 2013), but may also lead to an increase in the incubation period of long-tailed tits, potentially increasing the risk that hatching is mis-timed relative to peak availability of caterpillars (Burgess et al., 2018).

Weather variables had marginal negative consequences because they had negligible effects on hatching success and led to a smaller change in the probability of nest predation, through increased exposure time, compared with the changes due to clutch size and timing of breeding. While, exposure time only provides limited information about the predation risk that a brood may face as predator behavior can change in relation to weather conditions (Morrison and Bolger, 2002; Preston and Rotenberry, 2006) there is no evidence that predation rates of long-tailed tit nests is related to weather in our study system (Gullett et al., 2015).

The negligible effect of temperature on hatching success is somewhat surprising given that other studies have found that lower ambient temperature can affect egg viability (Beissinger et al., 2005; Ardia et al., 2006). Contrary to our predictions and other studies (MacDonald et al., 2013; Martin et al., 2017), rainfall also had only a negligible effect on hatching success. These minor effects of environmental conditions on hatching success suggest that long-tailed tits may be able to buffer adverse weather conditions, either through females altering their incubation behavior or through the construction of well-insulated and water-resistant nests. Alternatively, it may be that for long-tailed tit embryos a reduction in temperature does not lead to the death of the embryo, but does lead to slower embryo development, which causes a lengthening of the incubation period. Further investigation is required to test these hypotheses.

Other factors had important impacts on hatching success. First, hatching success decreased as the incubation period increased, a finding consistent with previous studies of blue tits (Kluen et al., 2011; Nord and Nilsson, 2011), tree swallows (Lombardo et al., 1995), and great tits (Diez-Méndez et al., 2020). These results indicate that while birds may extend incubation to delay hatching so that it coincides better with the peak of food abundance, there is a cost to this strategic decision if it reduces hatching success. The relationship between hatching success and incubation period could be the result of either decreasing egg viability with time or increased fluctuation in egg temperature causing a reduction in egg viability. Support for the incubation inefficiency explanation is equivocal. An experimental study of house wrens *Troglodytes aedon* that used cross-fostering of eggs to extend or reduce the length of time females had to incubate a clutch had no effect on hatching success (Sakaluk et al., 2018), suggesting that the inefficient incubation hypothesis is unlikely. However, females in lower body condition incubate for longer and have reduced hatching success due to lower incubation temperatures (Hepp et al., 2006) and increased incubation recesses (Bueno-Enciso et al., 2017). In addition, Nord and Nilsson (2011) found that when incubation temperature was low, the incubation period was extended and the hatching success was lower. These mechanisms are not mutually exclusive, and either could result in the observed decrease in long-tailed tit hatching success.

We also found a weak, positive relationship between hatching success and clutch size. This contrasts with experimental studies reporting lower hatching success with increased clutch sizes (Siikamiiki, 1995; Reid et al., 2000b), which was presumed to be attributable to energetic constraints on successful incubation of experimentally enlarged clutches, as already discussed. The contrast between our observational findings and previous experimental studies may be explained by better quality females having larger clutch sizes and being better able to maintain the incubation temperatures (Hepp et al., 2006), leading to higher hatching success.

Finally, we found that hatching success was lower for older females. Previous work on putative age effects is equivocal. Some studies report increasing hatching success with age, e.g., prothonotary warblers *Protonotaria citrea* (Blem et al., 1999), while others have found no effect, e.g., European starlings *Sturnus vulgaris* (Komdeur et al., 2005), blue tit (Lambrechts et al., 2012) and house sparrows *Passer domesticus* (Stewart and Westneat, 2013). Our results are consistent with senescence, which has been widely reported in passerine reproductive performance (Monaghan et al., 2008; Robertson and Rendellt, 2012; Jankowiak and Wysocki, 2016), but it should be noted that in previous studies, albeit based on smaller sample sizes, we have not detected senescence in long-tailed tit life history traits (Hatchwell et al., 2004; Meade and Hatchwell, 2010).

In conclusion, our long-term analysis showed that mean daily temperature, proportion of rainy days, clutch size and relative incubation start date explained variation in the duration of the incubation period of long-tailed tits. In contrast, we found only marginal effects of environmental conditions on hatching success. This suggests that wet conditions cause slower growth of embryos and hence longer incubation periods, rather than directly causing embryo fatality. Finally, long incubation periods were likely to be costly due to reduced hatching success and increased exposure to predation risk.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by University of Sheffield Ethical Review Committee (Project Applications and Amendments Sub-Committee) and a Project License is held for taking blood samples from the UK Home Office (PPL 70/8434).

AUTHOR CONTRIBUTIONS

CGH is supervised by KLE and BJH who initiated and manages the long-term long-tailed tit study system. CGH led the data analysis and wrote the first draft of the manuscript. KLE and BJH contributed to the conception and design of the data analysis, interpretation, and writing the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.542179/full#supplementary-material

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Associations of Synoptic Weather Conditions With Nocturnal Bird Migration Over the North Sea

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The southern North Sea is part of an important flyway for nocturnal bird migration, but is also risky as it stretches over a large surface of water. Selecting nights with suitable weather conditions for migration can be critical for a bird's survival. The aim of this study is to unravel the weather-related bird migration decisions, by providing a descriptive analysis of the synoptic weather conditions over the North Sea on nights with very high and low migration intensities and compare these conditions to the prevailing climatology. For this study, bird radar data were utilized from an offshore wind farm off the Dutch coast, in the North Sea. The study suggests that atmospheric conditions clear of rain and frontal systems, dominated by high pressure systems and tailwinds in spring and sidewinds in autumn are most suitable for nights of intense migration. Differences in temperature, relative humidity and cloud cover appear less significant between intense and low migration nights, suggesting that these variables exert only a secondary role on migration. We discuss how future developments in radar aeroecology and the integration of meteorology can help improve our ability to forecast bird migration.

Keywords: bird migration, synoptic weather, North Sea, radar observations, radar data

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INTRODUCTION

Twice a year large flows of terrestrial birds migrate over the North Sea during the night (Lack, 1963a,b; Hüppop et al., 2006; Hüppop and Hüppop, 2011; Shamoun-Baranes and van Gasteren, 2011). The crossing mainly occurs between the lowlands of Netherlands and Germany and Norway (cca 540 km), Denmark and Netherlands (cca 300 km) and between United Kingdom and Netherlands (cca 200 km) (Lack, 1959; Shamoun-Baranes and van Gasteren, 2011; Bradarić et al., 2020). To cross such distances, a bird with the average airspeed of 16 m/s needs between 3.5 and 10 h in still air. Since such large water bodies are not suitable for resting and refueling for many terrestrial migrants, the trip is considered risky for migration, especially if at the same time birds have to cope with unfavorable weather conditions. It is therefore important for migrating birds to select nights with atmospheric conditions that support migration (Richardson, 1978). An addition to the risk posed by encountering inclement weather en route is the risk of collisions with large man-made structures, such as wind turbines developed within migratory flyways (Brabant et al., 2015; Fijn et al., 2015; Aschwanden et al., 2018; Thaxter et al., 2019). Nowadays the production of wind energy experiences a rapid expansion, as the necessity to reduce reliance on fossil fuels is large in order to mitigate the risks from human-induced climate change. To reduce chances of bird collisions the temporary shutdown of wind turbines is one of the mitigation measures suggested to reduce collision risk when bird migration intensities are high (May et al., 2015). In order to design effective and sustainable early warning systems a good understanding of migratory behavior is needed (Bauer et al., 2017).

During migration, daily numbers of birds in the air can fluctuate by orders of magnitude, and studies have shown that temporal variation in migration intensity can be explained in part by local weather conditions (Richardson, 1978; Erni et al., 2002; Van Belle et al., 2007; Shamoun-Baranes et al., 2017). Among diverse atmospheric variables, wind speed and direction is often considered the most influential for nocturnal migrants and especially passerines using flapping flight (Bruderer et al., 1995; Erni et al., 2002; Van Belle et al., 2007; Sjöberg et al., 2015), as with greater wind support travel time and energy expenditure are minimized (Liechti et al., 2000; Schmaljohann et al., 2009). The influence of wind on migratory birds is often discussed in terms of head and tailwinds along a preferred migration direction and sidewinds perpendicular to the preferred migration direction. It has been demonstrated that nocturnal passerine migrants have the ability to partially compensate for the side wind drift during their journey (Alerstam, 2011; McLaren et al., 2012; Chapman et al., 2016), but they tend to follow paths where they have to compensate less (Horton et al., 2016). Studies have shown that numbers of birds aloft (e.g., Erni et al., 2002; Van Belle et al., 2007) as well as probability of departure of passerines (Åkesson and Hedenström, 2000; Schaub et al., 2004; Sjöberg et al., 2015) is higher on nights with supporting winds.

There is evidence that precipitation is another key factor for migrants as it may temporarily suppresses migration (Richardson, 1978; Schaub et al., 2004). Rain might increase the risk of mortality as it decreases visibility and increases disorientation for birds en route (Newton, 2007). However, the impact of precipitation on departure decisions is not always clear, for example while Schaub et al. (2004) found decreased departure chances of small passerines during precipitation, Andueza et al. (2013) did not find an important effect of precipitation on departure decisions of migrating passerines. Cloud cover and temperature, have also been shown to influence departure decisions. For example a radio telemetry study showed that yellow-rumped warblers *Setophaga coronata* were more likely to depart from stopover sites (i.e., rest and refueling sites) in autumn in clear skies than overcast (Liu and Swanson, 2015) with temperature having less of an impact on departure decisions. The relative importance of weather variables may vary between spring and autumn as the prevailing weather conditions differ. For example, the passage of high-pressure systems can be related to opposing winds in autumn and supporting winds in spring (Dokter et al., 2013). Additionally, species with similar flight modes but contrasting migration strategies, for example short vs long distance passerines may respond differently to weather conditions at departure (Packmor et al., 2020). As many weather variables are closely intercorrelated, less influential variables such as the relative humidity will tend to vary in predictable ways as a function of the variables of higher importance, such as the pressure systems (Richardson, 1990), or precipitation, especially during relatively unstable atmospheric conditions.

The advancement of radar technology has greatly facilitated studying nocturnal migration even though radar systems cannot distinguish patterns and characteristics of migration at a species level (Bauer et al., 2019). The aim of this study is to increase our understanding of how weather influences mass migration events over the sea. The study compares synoptic scale weather conditions to climatology on nights of very high migration intensities and nights of very low migration intensities over the North Sea. In order to study conditions during migration within the context of seasonal weather conditions, we calculate the climatological anomalies of several key weather variables. The weather conditions associated with the selected high migration intensity nights should indicate conditions that favor migration. Respectively the weather conditions associated with the low migration nights should indicate the conditions that might inhibit migration for the specific latitude and geography over the North Sea. The key variables of interest follow suggestions from previous research (Richardson, 1990) and include: winds at 925 hPa, mean sea level pressure (MSLP), 500 hPa geopotential height, precipitation, relative humidity, cloudiness, and temperature. Furthermore, using surface synoptic weather maps, we explore the passage of frontal systems on nights of high and low migration intensity. The research is based on spring and autumn bird radar observations made 18 km from the Dutch coast, in the North Sea, and the concurrent synoptic weather conditions over sea and in potential departure areas. We expect that intense peaks and lulls in migration observed over sea will be strongly influenced by weather conditions at potential departure areas over land during the night of interest. Previous studies of passerine migration have shown that seasonal phenology at stopover sites can be strongly influenced by weather conditions at distant stopover or overwintering areas in spring (Haest et al., 2018) and distant stopover or breeding ranges in autumn (Haest et al., 2019). Thus, we describe the synoptic scale conditions in relation to potential departure areas on nights of high migration intensity. A back-trajectory analysis of migration using the same radar dataset (Bradarić et al., 2020) showed that the most probable departure areas of the birds on nights of high migration intensity observed at the radar site in spring is southern United Kingdom (area in blue circle in **Figure 1**) and in autumn is Southern Scandinavia, the north coast of Netherlands and Germany (area in red circle in **Figure 1**). We discuss similarities and differences between spring and autumn in synoptic scale conditions that support or potentially inhibit migration over the southern North Sea.

DATA AND METHODS

Radar Observations of Migration

We utilize data collected for previous projects (Krijgsveld et al., 2005, 2011; Fijn et al., 2015), recorded by a Merlin radar system (DeTect Inc., Panama City, FL, United States) which

FIGURE 1 | The map of study area around the North Sea. The star indicates the position of Egmond aan Zee wind farm, where the radar is located. The blue circle indicates the most probable departure area of the migrants on nights of high migration intensity in spring. The red circle indicates the most probable departure area of the migrants on nights of high migration intensity in autumn outside of the Netherlands according to Bradarić et al. (2020).

was mounted on a meteorological mast of the Egmond aan Zee Offshore Wind Farm (OWEZ) (N 52.60, E 4.38) located 18 km off the Dutch NW coast (location shown in **Figure 1**). The radar system consisted of two marine surveillance radars that allow detection of individual bird echoes. A vertical X-band Furuno radar scanned the area along a NW-SE direction at speed of 25 rpm and detected biological objects within a detection range of ∼1.4 km from the radar (vertical extent). A horizontal S-band Furuno radar with a detection range of 5.5 km scanned an area of 360° around the radar at a speed of 22 rpm. The detection of targets by the radar system depends on their size, distance from the radar and orientation relative to the radar beam. Measurements showed that effective detection of the Merlin system varied between 900 and 1.4 km for the vertical radar and between 900 m and 4.5 km for the horizontal radar, depending on the previously mentioned factors. Small birds were successfully detected up to an altitude of 900 m.

We utilized radar data collected from June 2007 until May 2010. The radar was operational 90% of the time, except for short breaks caused by technical failure, weather conditions that could have caused mechanical damage of the radar (wind speed >14 m/s) or disrupt detection of targets (rain) and maintenance. The vertical radar recorded numbers of targets that were crossing the radar beam and their altitudes. The horizontal radar collected information about ground speeds and track directions of the targets. Extensive field measurements of the radar performance (Krijgsveld et al., 2005) which included visual identification of targets and their flagging in the database allowed for detailed post processing of the data. Filters based on echo characteristics of targets such as speed, direction and size were developed (Krijgsveld et al., 2011). These filters were used to exclude echoes originating from waves, rain, insects and other types of interference (e.g., boats). For more information about data quality, filtering procedures and the quantification of fluxes see Krijgsveld et al. (2011) and Fijn et al. (2015).

Using track directions and ground speeds recorded by the horizontal radar and hourly u and v components of 925 hPa wind from the ERA5 data described below, airspeeds (speed of a bird in still air) and headings (direction of a bird in still air) at the radar location were calculated using vector summation (Shamoun-Baranes et al., 2007). Wind was analyzed at 925 hPa, since the radar used in this study recorded mainly birds flying below 1000 m of altitude (Fijn et al., 2015), and represents the altitude layer where migration intensity is highest in this region (Kemp et al., 2013). The wind data was linearly interpolated to the start time of tracks as recorded by the radar.

Selection of High and Low Migration Intensity Nights

In this study, the spring migration season was defined as 15 February–31 May and autumn migration season was defined as 1 August–30 November. For each night beginning around sunset and ending at sunrise the next day (18:00–06:00 UTC), we calculated the total number of tracks recorded by the vertical radar as a measure of migration intensity per night. We ranked nocturnal migration intensity in descending order and selected the nights exceeding the 90th percentile separately for spring and autumn, resulting in 24 spring and 22 autumn nights. If successive nights among them exceeded the 90th percentile threshold, then only the maximum night was included in this analysis, in order to avoid the analysis of dependent synoptic weather conditions, resulting in the final nine autumn and eight spring nights (called hereafter high migration nights). The 90th percentile was selected for statistical reasons, as with this threshold at least one case per year is selected and thus all years are represented in the analysis. Nights with very low migration intensity that occurred just before or just after the selected high migration nights were also selected, and called thereafter low migration nights. In total, eight nights with low migration were selected in autumn and seven in spring and occurred from 1 to 7 days before or after the high migration nights. The low migration nights on average had migration intensities that were 95% lower than the associated high migration nights. Nights in which the radar was not operational, were excluded from any selection. The selection of the nights with low migration intensity was made in order to investigate whether inhibiting weather precedes a high migration pulse, or pauses it (the nights after the high migration pulse). However, migration intensities might also be low in nights of favoring weather conditions, as the flying migrants also need to feed and rest, or simply because after nights of high migration intensity there are not many birds left in the source area (Gauthreaux et al., 2005).

All analysis of directional data was done using the R package *circular* (Agostinelli and Lund, 2017; R Core Team, 2018). Circular mean and ± angular deviation (AD) of track direction, heading and wind direction at the radar location were calculated per night. Furthermore, the mean resultant vector length r was estimated for each of the parameters to assess the dispersion of directional data around the mean (values closer to 1 indicate less dispersion). Finally, Rayleigh test was performed to test for non-uniformity of directional data (alternative hypothesis is unimodal distribution). Density distributions (**Figures 2**, **3**) of all directional data are kernel densities derived using *density circular* function.

Meteorological Data and Analysis

We used the recently released ERA5 reanalysis product from the European Centre for Medium-Range Weather Forecasts (ECMWF) (Hersbach and Dee, 2016) with hourly temporal and 30 km spatial resolution. The analyzed ERA5 variables were 925 hPa wind, MLSP, precipitation, geopotential height at 500 hPa (the height where the ridges and troughs are usually detected in the middle troposphere), relative humidity, cloudiness and 2 m temperature for three springs and three autumns for the years 2007–2010. As we are focusing on factors influencing nocturnal migration we calculated nightly means from 18:00 UTC of the day of interest until the next morning at 06:00 UTC. The nightly precipitation data is the total precipitation from 18:00 to 06:00 UTC. The local Dutch time is UTC+1 in winter and UTC+2 in summer. The weather variables were extracted from the spatial range of 35N–70N and 16W–19E. This entire region is plotted for the MSLP (**Figures 4**, **5**) to allow a clear overview of the passing synoptic scale pressure systems. The rest of the analyzed variables have more local character and are therefore plotted over the North Sea and the continental regions around it (**Figures 2**, **3**, **6**, **7**). Finally, the surface pressure and frontal systems are shown over a broader region as they are extracted from the KNMI data center (**Figures 8**, **9**).

The monthly climatology per grid point for spring and autumn migration was calculated as the monthly means from 18:00 to 06:00 UTC for the years 1989–2018. The emphasis of the current work is given on the relation between the synoptic weather conditions and bird migration. In order to understand the biological relevance of the synoptic wind directions though, the local wind directions at the radar site are first assessed and discussed in the context of bird headings and track directions measured by the radar. Afterward, the synoptic wind conditions are explored in conjunction with the bird headings and track directions on days of high and low migration. The synoptic wind conditions are computed by the intensities of the zonal and meridional wind vectors and the composites are the averages of the nightly means. In order to calculate the anomalies from climatology for MSLP, precipitation, geopotential height, relative humidity, cloud cover and temperature, the monthly climatology was subtracted from the selected nightly mean for each variable of interest. Then the spatio-temporal composite of the anomalies was calculated as the mean for the selected high and low migration nights, respectively. Additionally, the day-by-day surface pressure and frontal systems maps that are shown and discussed in the following sections are extracted from the Royal Netherlands Meteorological Institute (KNMI) and are taken at 18:00 of each day.

To assess whether the anomalies were statistically different from climatology, we applied the Welch's t-test for unequal variances and unequal sample sizes (Ahad and Yahaya, 2014). The test computes the mean and variance of the nightly values of the high (or low) migration nights and compares those to the nightly values of all 30 years of climatology, for the selected migration month, for each grid cell separately in the synoptic maps. If the p-value of each grid cell is below a selected threshold, then the null hypothesis can be rejected and the value in that grid cell is assumed significantly different from climatology. The selected threshold in this work was the 95% confidence level (p-value ≤ 0.05).

For the analysis of the meteorological data in this study we used CDO, Ferret and Python data visualization and analysis tools.

Regional Climatic Conditions

Here we provide a very brief overview of the climatic conditions in the region to issue the appropriate context for interpreting anomalies in synoptic conditions in relation to bird migration. In Spring climatologically dry and stable conditions dominate the southern United Kingdom and the southern North Sea as the passage of synoptic systems and frontal activity that is responsible for most of the large scale precipitation is less frequent and the sea is still too cold to induce local convection as it approaches the land (Manola et al., 2019). Most high pressure systems come from the Azores via the United Kingdom to Iceland or Scandinavia. With calm weather the levels of relative humidity and low cloudiness depend strongly on the atmospheric temperature. The sea surface temperature is at its lowest point of the year. In periods with south- or southwesterly winds, the relatively warm air condenses from the cold sea with fog and low clouds as a result.

In autumn and winter, storm tracks with low pressure and frontal systems are most active over the United Kingdom, the North Sea and Scandinavia/Denmark and the Low countries (Woth et al., 2006). The prevailing winds are westerlies and southwesterlies, the atmospheric conditions are very variable and the frequent passing of the frontal systems often bring a lot of rain.

RESULTS

Spring

Surface Winds and Bird Tracks

On nights of high migration intensity in spring, the average winds are southwesterly (61.47° ± 53.8°, $r = 0.55$, $p = 0.08$) and the track direction (79.75° ± 28°, $r = 0.87$, $p < 0.001$) and bird headings (84.47° ± 22.3°, $r = 0.92$, $p < 0.001$) point toward east and are significantly concentrated around the mean (**Figure 2A**). Considering the suggested departure locations and migratory axes in the North Sea basin, winds on high migration nights support migration from southern United Kingdom toward

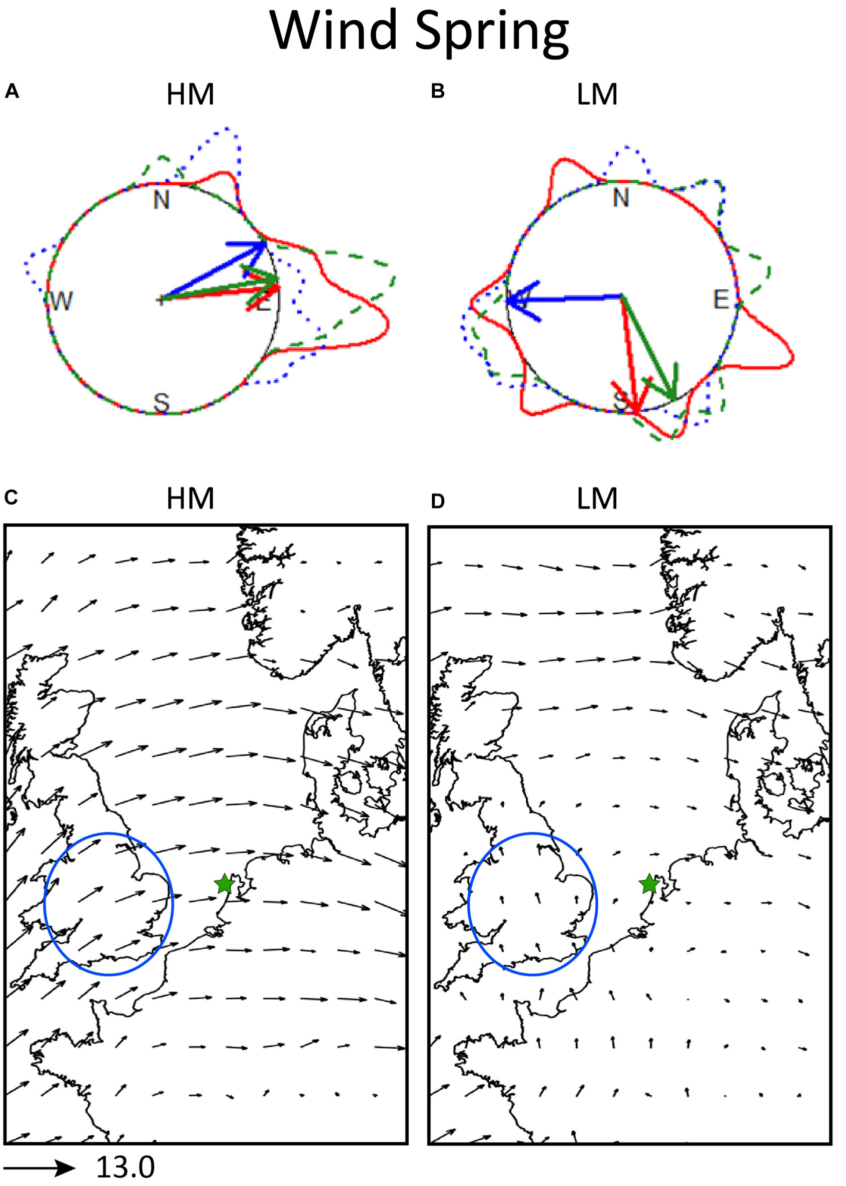

FIGURE 2 | Local and synoptic 925 hPa winds in spring. Top panel: Inside each circle, the mean heading of the birds (red arrows), mean 925 hPa wind direction at the radar location (blue arrows), and mean track direction of the birds (green arrows). Around the circle, the circular density distributions of bird heading (solid line), wind direction (dotted line), and track direction (dashed line), in panel **(A)** for nights of high migration intensity (HM) and in panel **(B)** for nights of low migration intensity (LM). Bottom panel: synoptic 925 hPa wind conditions in spring, in panel **(C)** for nights of high migration intensity (HM) and in panel **(D)** for nights of low migration intensity (LM). The length of the arrows is proportional to the strength of the averaged wind. As a reference the length of the arrow of 13 m/s wind strength is given under the panels. The circled area designates the most probable area of departure for the detected flying migrants during those nights. The star designates the location of the radar.

Netherlands as well as from the southern Europe toward Scandinavia on nights with intense migration activity. However, on nights with low migration intensity the winds are on average easterlies, but not signficant due to high variability in wind direction (267.67° ± 70°, $r = 0.25$, $p = 0.7$). The track directions (153.43° ± 68°, $r = 0.26$, $p = 0.6$) and bird headings (173° ± 68°, $r = 0.25$, $p = 0.7$) are also highly variable and on average point toward south (**Figure 2B**). The high variability of wind on low migration nights can also be seen in the synoptic winds map in **Figure 2D**, as the averaging of the different wind directions results in low intensity winds of rather unclear directions.

Pressure Systems and Fronts

In spring the MSLP composite of the high migration nights is characterized by an extended ridge of high pressure from Spain into Central Europe (**Figure 4A**), bringing overall dry conditions over most parts of Western and Central Europe, the North Sea and southern United Kingdom. The anomalies

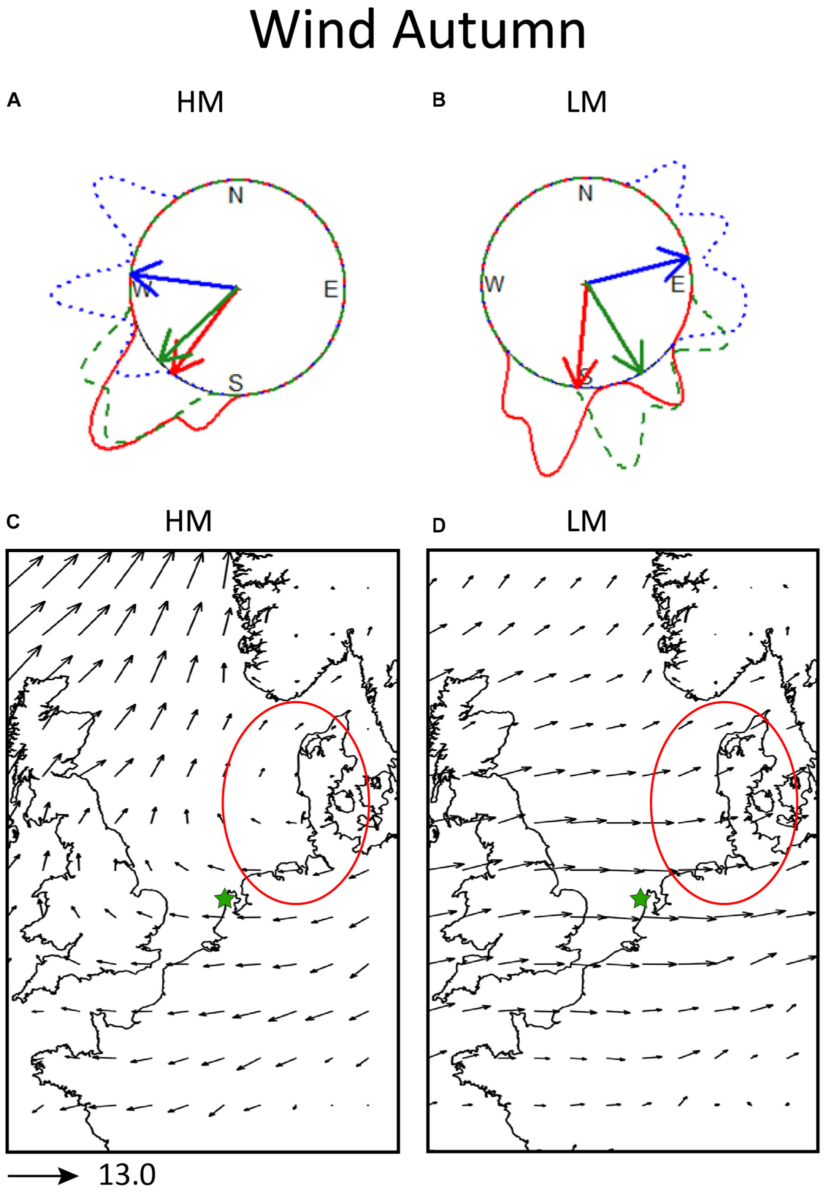

FIGURE 3 | Local and synoptic 925 hPa winds in autumn. Top panel: Inside each circle, the mean heading of the birds (red arrows), mean 925 hPa wind direction at the radar location (blue arrows) and mean track direction of the birds (green arrows). Around the circle, the circular density distributions of bird heading (solid line), wind direction (dotted line) and track direction (dashed line), in panel **(A)** for nights of high migration intensity (HM) and in panel **(B)** for nights of low migration intensity (LM). Bottom panel: synoptic 925 hPa wind conditions in autumn, in panel **(C)** for nights of high migration intensity (HM) and in panel **(D)** for nights of low migration intensity (LM). The length of the arrows is proportional to the strength of the averaged wind. As a reference the length of the arrow of 13 m/s wind strength is given under the panels. The circled area designates the most probable area of departure for the detected flying migrants during those nights. The star designates the location of the radar.

do not differ significantly from regional climatology, indicating that the climatic conditions for this region are supportive of migration over the North Sea in the study region. Along the western flank of this ridge, over the North Sea and southeastern United Kingdom the winds have a southerly or southwesterly component (**Figure 2C**). It should be noted that at the mid-latitudes the winds blow approximately parallel to the isobars, having the low pressure to their left in the Northern hemisphere. The surface pressure and frontal systems for all high and low migration days are shown in **Figure 8**. When the surface pressure, that on average creates the favoring wind conditions seen in **Figure 2C**, is studied individually for each of the high migration nights we observe several different patterns: (1) high pressure observed over the southern United Kingdom and the Dutch coast on three nights (see pressure isobars in **Figures 8B,D,F**), (2) the study site at sea is positioned between

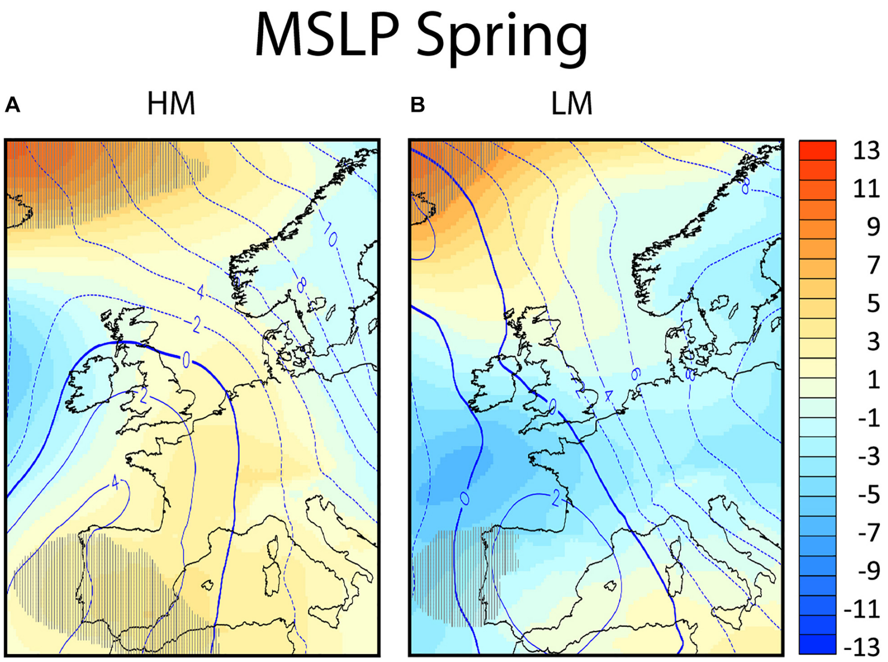

FIGURE 4 | The composites of the anomalies from climatology for spring migration for the mean sea level pressure (MLS P in hPa, in colors) and for the 500 hPa geopotential height (in decameters, in contours) in panel **(A)** for nights of high migration intensity (HM) and in panel **(B)** for nights of low migration intensity (LM). Areas exceeding the 95% confidence level as concluded by the Welch's *t*-test are hatched.

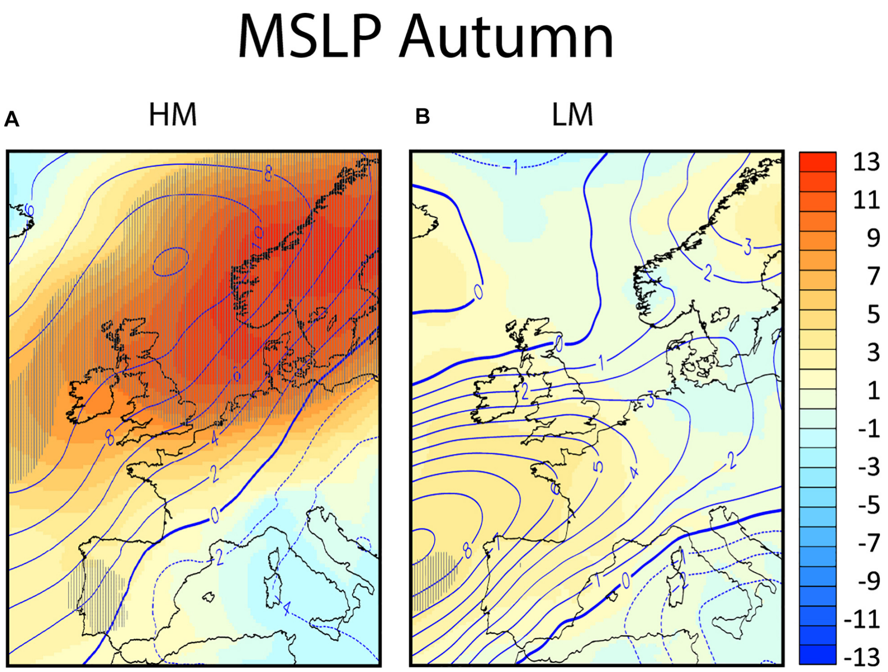

FIGURE 5 | The composites of the anomalies from climatology in autumn for the mean sea level pressure (in hPa, in colors) and for the 500 hPa geopotential height (in decameters, in contours) in panel **(A)** for nights of high migration intensity (HM) and in panel **(B)** for nights of low migration intensity (LM). Areas exceeding the 95% confidence level are hatched.

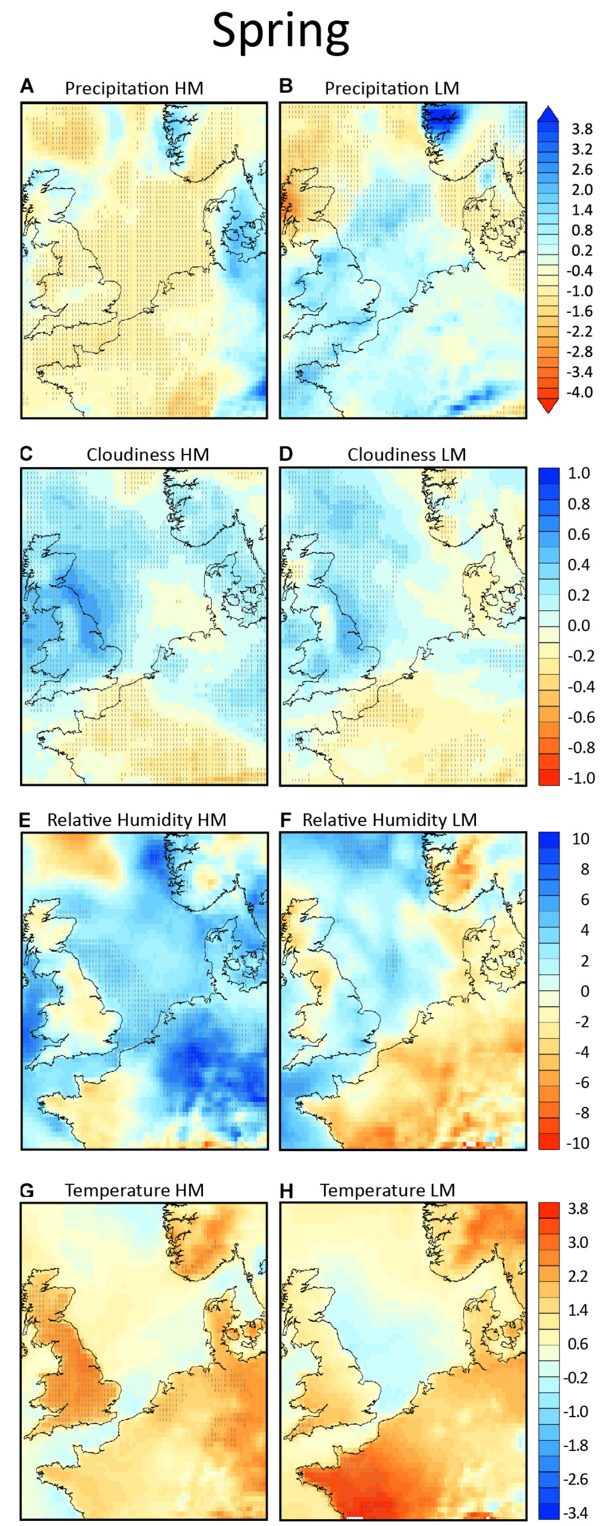

FIGURE 6 | Composites of anomalies from climatology in spring, in the left column for the high migration nights (HM) and in the right column for the low migration nights (LM). In panels **(A,B)** the total precipitation (in mm) is shown, in panels **(C,D)** the total cloud cover (units from –1 to +1), in panels **(E,F)** the relative humidity (in %) and in panels **(G,H)** the 2 m temperature field (in °K). Areas exceeding the 95% confidence level are hatched.

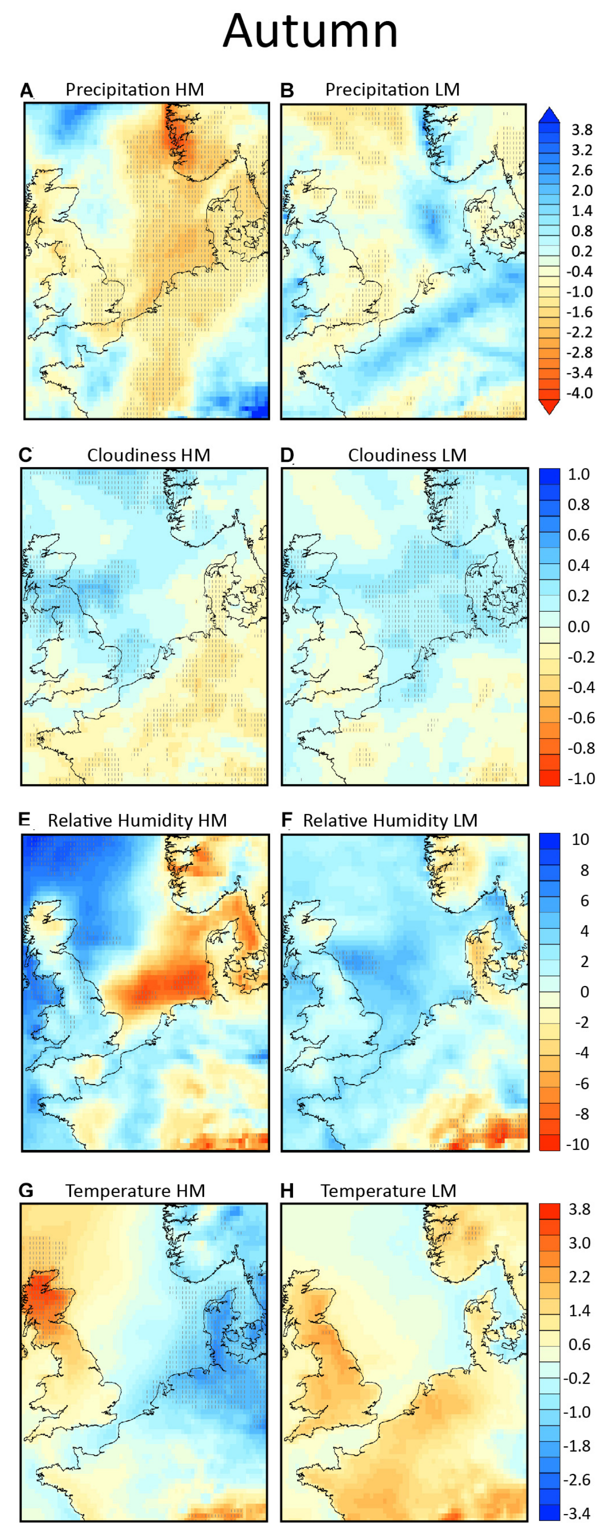

FIGURE 7 | Composites of anomalies from climatology in autumn, in the left column for the high migration nights (HM) and in the right column for the low migration nights (LM). In panels **(A,B)** the total precipitation (in mm) is shown, in panels **(C,D)** the total cloud cover (units from –1 to +1), in panels **(E,F)** the relative humidity (in %) and in panels **(G,H)** the 2 m temperature field (in °K). Areas exceeding the 95% confidence level are hatched.

low and high pressure systems on three nights (see isobars and the location of the core of the high and low pressure systems indicated with H or L, respectively (**Figures 8C,E,G,H**) and (3) a low pressure system observed over the North Sea on one night (**Figure 8A**). The individual high migration nights are characterized by the general absence of frontal systems over the coast of Netherlands, apart from the 14th of March 2010 when a long but weak and dry cold front passed over the North Sea (**Figure 8E**).

On the other hand, the composite of the low migration nights shows a non-significant low surface pressure anomaly over the southern North Sea, that leaves the coast of Netherlands close to the climatological average surface pressure (**Figure 4B**). The anomalies over sea and potential departure areas do not differ significantly from regional climatology. Among the low migration nights, the Dutch coast is positioned during three nights over low pressure systems (**Figures 8I,J,L**), during two nights between high and low pressure systems (**Figures 8K,O**), and during two nights over high pressure systems (**Figures 8M,N**). During all low migration nights a front (warm, cold or occluded) or a trough passes over the coast of Netherlands or the southern United Kingdom.

Precipitation, Relative Humidity, Cloudiness and Temperature

In high migration nights potential departure locations in the United Kingdom arrival locations on continental Europe, as well as the North Sea are considerably drier compared to the monthly climatological conditions (**Figure 6A**), and considerably wetter in the low migration nights (**Figure 6B**). The dry anomalies during the high migration nights are statistically significant over almost the entire area (hatched areas in **Figure 6**), while the wet anomalies during the low migration nights over the areas of interest are non-significant. When the individual days are examined (not shown) it is observed that during all high migration nights the conditions are dry, while during low migration nights rain occurs in at least one of the areas of interest for each night.

Cloud cover is closely related to precipitation, but can also occur independently. Neutral to negative non-statistically significant anomalies in cloudiness over the Dutch coast, in **Figures 6C,D** are consistent with the absence of rain during the high migration. Areas of statistically significant increased cloudiness compared to climatology over southern United Kingdom indicates that the birds might also fly into cloudy, but dry skies. The above indicate the partly decoupled behavior between cloudiness and precipitation (as they don't necessarily co-occur), while they also indicate a secondary role of cloudiness in the bird's migration decisions.

As precipitation and relative humidity are closely intercorrelated, especially under unstable atmospheric conditions, we examine whether the birds appear to respond to relative humidity as they might use it as an early indicator for rain. Relative humidity over southern United Kingdom does not differ signficantly from the local climatology on high migration nights, but is significantly higher over the coast of Netherlands (**Figure 6E**). During low migration nights the pattern is reversed, with somewhat higher (non-significant) relative humidity over southern United Kingdom and lower over Netherlands (**Figure 6F**). Surface temperature is also not signficantly different over the entire continental region of the map during both high and low migration nights (**Figures 6G,H**).

Autumn

Surface Winds and Bird Tracks

On nights of high migration intensity the prevailing winds at the radar location were easterlies (277.05° ± 26.9°, $r = 0.88$, $p = 0.01$), while headings (217.57° ± 11.4°, $r = 0.97$, $p = 0.02$) and track directions (227° ± 11.4°, $r = 0.97$, $p < 0.001$) were toward southwest. During nights of low migration intensity the winds blew on average from the west (84.47° ± 0.39°, $r = 0.92$, $p < 0.001$), while the mean track direction toward southeast (148.48° ± 0.38°, $r = 0.92$, $p = 0.01$) and the mean heading (185.27° ± 0.43°, $r = 0.9$, $p = 0.02$) toward south. The local wind directions were more concentrated around mean on nights of low migration intensity nights. On nights with high migration the track directions and headings were more concentrated around their mean value, compared to nights with low migration activity.

Overall, the synoptic winds in autumn (**Figures 3C,D**) were favorable for crossing between Netherlands and United Kingdom on nights of high migration. However, the average track directions and headings suggest that the majority of tracks recorded by the radar were moving more to the SW and indicating birds flying predominantly parallel to the coast rather than crossing directly to the United Kingdom at the radar location.

Pressure Systems and Fronts

Nights of high migration are characterized by an elongated high-pressure anomaly centered over southwest Scandinavia, extending to the British Isles (**Figure 5A**). The 500 hPa geopotential height (the contour lines of **Figure 5A**), shows an upper ridge from the United Kingdom into Scandinavia. This will lead to mostly northeasterly or easterly winds over southern Scandinavia, Denmark and Netherlands, confirmed in **Figure 3C**. The MSLP anomaly is statistically significant over the entire area of interest (over sea and the potential departure area). The pressure anomaly reaches a maximum of 12 hPa near the potential departure area. High pressure systems are observed over the Dutch coast on almost all the high migration intensity nights (**Figures 9A–E,G–I**), resulting in the averaged easterly winds seen in **Figure 3C** over Netherlands. A lack of frontal systems is apparent over the Dutch coast and southwest Scandinavia. An exception is the 30th of October 2009 where a front passes over the North Sea between Netherlands and Denmark (**Figure 9H**), though that systems was dry and did not render any precipitation. During October 29, 2008 and November 8, 2009 (**Figure 9F,I**, respectively), a trough over the North Sea result in some mild precipitation.

On the other hand, the composite of the low migration intensity nights is characterized by a zonal flow with a slight southwest-northeast angle. This spatial pattern characterizes also the Autumn North Europe climatology. The MSLP anomalies are quite low and non-significant, while some positive

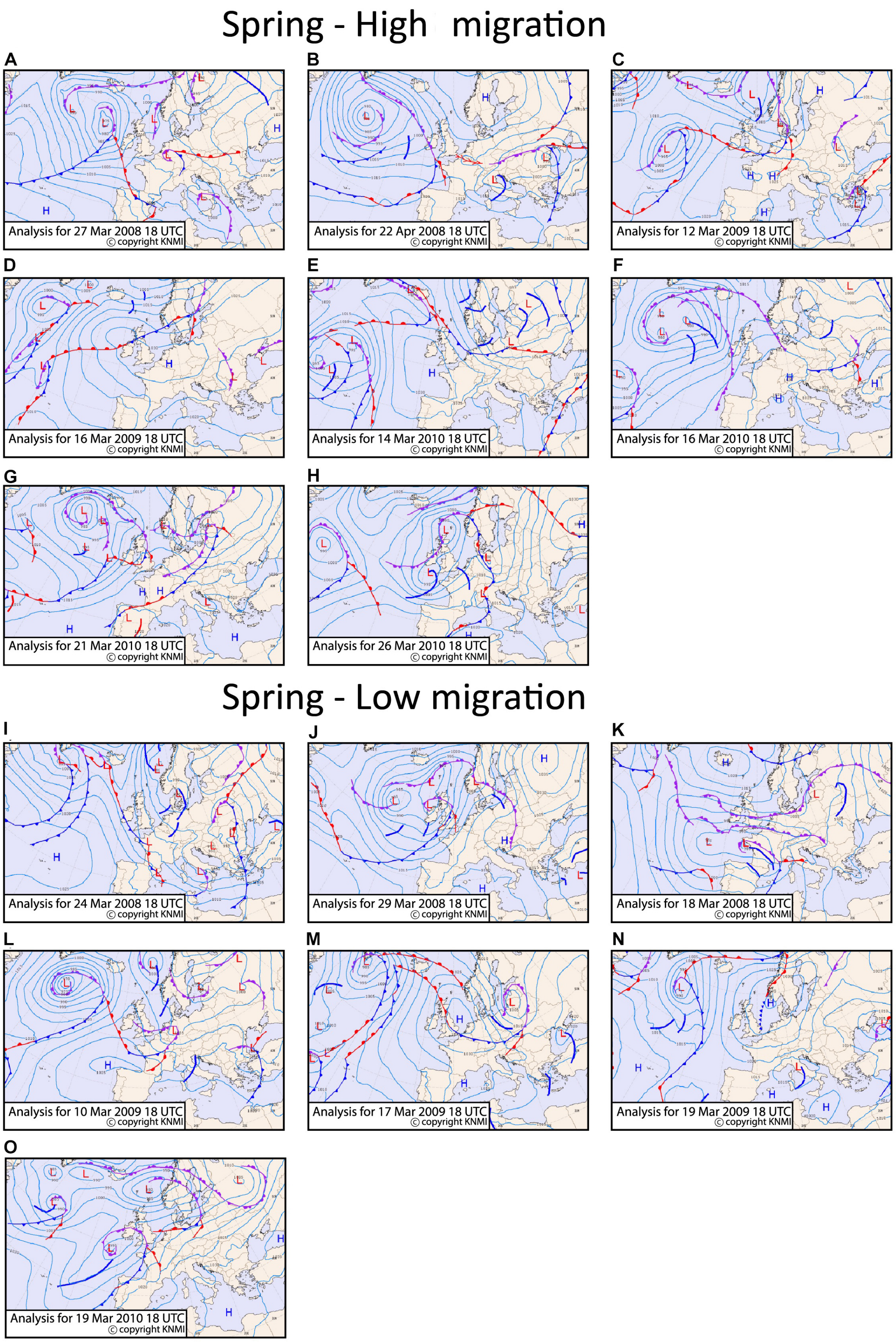

FIGURE 8 | Surface pressure and frontal systems for the high migration nights **(A–H)** and the low migration nights **(I–O)** for spring at 18:00 UTC. The figures are extracted from KNMI data center. The position of the core of a low pressure system is indicated with an "L" and of a high pressure system with an "H." The cold fronts are indicated as lines in blue color, the warm fronts in red color and the occluded fronts in purple color. The side where the symbols are drawn on the front lines indicate the direction of the front's movement. The thick blue lines indicate troughs.

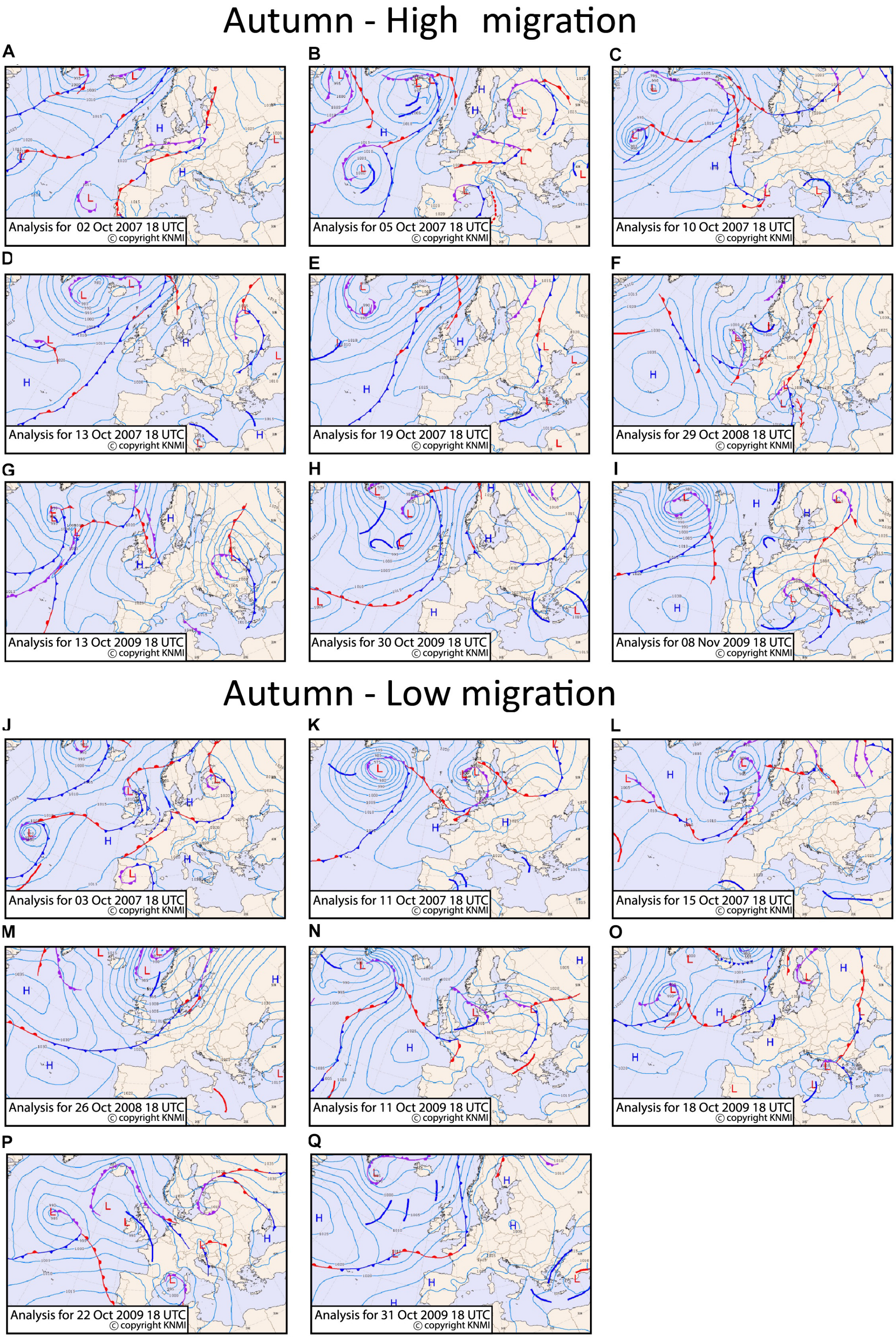

FIGURE 9 | Surface pressure and frontal systems for the high migration nights **(A–I)** and the low migration nights **(J–Q)** for autumn at 18:00 UTC. The figures are extracted from KNMI data center. The position of the core of a low pressure system is indicated with an "L" and of a high pressure system with an "H." The cold fronts are indicated as lines in blue color, the warm fronts in red color and the occluded fronts in purple color. The side where the symbols are drawn on the front lines indicate the direction of the front's movement. The thick blue lines indicate troughs.

500 hPa anomalies are seen west of the Iberian Peninsula and along northwest Europe (**Figure 5B**). A close look into the individual low migration days (**Figures 9J–Q**) shows that frontal systems pass during all low migration nights, either over Netherlands, North Sea, or potential departure areas (Denmark and Southwestern Scandinavia), indicating that the passing of fronts hinders migration.

Precipitation, Relative Humidity, Cloudiness and Temperature

In autumn during nights of high migration very little to no rain falls over the regions of the potential departure areas of the southern North Sea (Netherlands, Denmark, and south Scandinavia). The composite of the negative precipitation anomalies in these areas are statistically significant (**Figure 7A**). On the contrary, on all low migration nights precipitation is higher than expected in these areas (**Figure 7B**). During high migration nights, in agreement with the absence of rain over the coast of Denmark and continental Europe low cloudiness is observed, but over central North Sea the cloudiness is somewhat higher than the local monthly climatology (**Figure 7C**). During low migration, cloudiness is generally higher than in climatology and anomalies are statistically significant (**Figure 7D**), as rainfall occurs during those nights. Over the North Sea relative humidity is quite low on high migration nights and neutral to high, but non-statistically significant during low migration, while it remains low over Denmark and high over Netherlands both during high and low migration (**Figures 7E,F**). The surface temperature was statistical significantly colder than in climatology during nights of high migration both over sea and land over Denmark and Netherlands (**Figure 7G**). The colder temperature is related to the upper ridge seen in the 500 hPa geopotential height from the United Kingdom into Scandinavia that drives northeasterly winds which advect cold air from northeastern Scandinavia. During low migration nights the temperature was warmer over land and similar to climatology over the sea (**Figure 7H**).

SUMMARY AND DISCUSSION

Using 3 years of bird migration data measured off the Dutch coast, we revealed differences in the synoptic weather conditions occurring during high and low migration intensity nights in spring and autumn.

Nights of high migration intensities for both spring and autumn were characterized by prevailing high pressure systems, with a general absence of passing fronts and precipitation over sea and the probable departure areas over land. Generally, a high-pressure system is associated with dry and stable atmospheres, clear skies and mild winds. On the contrary, nights of low migration were characterized as nights with rain, often with passing fronts and overall low pressure. In spring a t-test shows that the positive surface pressure anomalies over sea and departure areas were not statistically significant, while in autumn the positive anomalies were significant. This suggests that the favoring migration conditions in spring are rather close to the average surface pressure climatology for that season, but in autumn more special conditions are required compared to the average climatology. The MSLP anomalies during low migration nights both in autumn and spring were not statistically significant, suggesting either a weak coupling between synoptic pressure systems and nights of low migration, or a combination of nights with unfavorable synoptic conditions for migration and nights of resting and feeding that might be decoupled from the synoptic pressure systems.

Our study shows that conditions free of precipitation support mass migration events. However, when using radar to measure migration it should be taken into consideration that during rain the ability of the radar to detect biological targets might be reduced and therefore the number of birds flying during rain may be underestimated. Nevertheless, even considering a potential underestimate of bird numbers, our findings are similar to previous studies indicating that rain strongly suppresses migration (Alerstam and Bauer, 1973; Lyuleeva, 1973) and is an important predictor variable for bird migration (Erni et al., 2002; Van Belle et al., 2007).

In spring, prevailing winds at the radar location, as well as in the whole region generally had a supporting direction for nocturnal migrants, which has previously been shown in this region (Kemp et al., 2013). During autumn nights with high migration the average winds at the radar location were tailwinds for the birds who could have been migrating between Netherlands and United Kingdom, while the majority of birds on high migration nights were migrating toward the southwest and thus experiencing sidewind component stronger than the tailwind on those nights. On nights with low migration intensity, winds at the radar location were predominantly headwinds in both seasons, indicating that tailwind is an important factor supporting migration, as also shown in numerous other studies (Liechti et al., 2000; Erni et al., 2002; Schmaljohann et al., 2009; Sjöberg et al., 2015). While the majority of migration happens within the lowest 1000 m of altitude in the mid-latitudes (Kemp et al., 2013; Bruderer et al., 2018), birds have also been observed flying higher to optimize wind support, especially in spring when beneficial wind at high altitudes are frequent (Dokter et al., 2013; Kemp et al., 2013). In such cases, high flying migrants would go undetected by the radar.

Since cloudiness is often linked to precipitation, it is observed here that birds prefer clear skies, although occasions of cloudiness during high migration flows also occur in our data. Interestingly warm south southwesterly winds which support migration in spring may also result in fog and low clouds generated by the condensation of warm air over the sea, creating poor visibility conditions. Studies have shown that birds might attempt to migrate above fog or clouds during overcast or rainy nights (Emlen, 1974; Panuccio et al., 2019). However, the occurrence of such behavior may not be detected by the radar if birds fly above the vertical detection range.

Although the absolute anomalies of the temperature and relative humidity are rather high in the analysis, the anomalies are not consistent for the two seasons. For example during high migration nights the anomalies of surface temperature over the areas of interest are positive in spring and negative in autumn. This suggests that the birds rather respond to factors that correlate with these variables and themselves exert only a secondary role, in agreement with Richardson (1978, 1990). The selection for cold temperature has been previously suggested as an indicator of deteriorating conditions and therefore as a signal for migration (Alerstam, 1990), but this suggestion cannot be verified in the current study.

Our selection of peak nights of migration above the 90th percentile per season resulted in high migration nights occurring in March and October. While we do not have information on the species in our study, the timing of these nights suggests that they may be generally representative of short to medium distance migrants in the region. Packmor et al. (2020) for example showed that night to night departure decisions of a short and medium distance migratory passerine was influenced by tailwinds and change in barometric pressure, while these weather factors did not influence departure decisions of a long distance migrants. However, in order to determine whether differential response to weather among and perhaps even within species results in peak migration over the North Sea occurring predominantly in early spring or late autumn requires further research integrating information on fluxes, species composition and regional synoptic conditions.

Our overall conclusion is that peak nights of bird migration over the North Sea are favored by the existence of high-pressure systems and the absence of fronts and are hindered by low-pressure systems and precipitation, in agreement with Geil et al. (1974), Richardson (1978), and Shamoun-Baranes et al. (2017). Winds on high migration nights in spring are tailwinds (southwesterlies), while in autumn they were sidewinds (easterlies). These patterns are similar to those observed in other studies in the region over land (Åkesson and Hedenström, 2000; Erni et al., 2002; Van Belle et al., 2007). In order better understand how environmental factors influence the spatio-temporal heterogeneity in migratory systems and improve our capacity to model them we recommend integrating complementary measurement and modeling techniques and covering longer periods of time where feasible (Shamoun-Baranes et al., 2010; Bauer et al., 2017). Incorporating information on species composition will significantly advance the comprehension of the potentially different responses to weather. Predictive models could integrate the synoptic scale perspective, considering the atmospheric conditions in departure areas of migrants, as well as atmospheric conditions en route in comparison to regional climatology. These advancements will consequently enhance our ability to predict migration flows and will allow us to build effective warning systems to reduce human wildlife conflicts such as risk of collisions with aircrafts (van Gasteren et al., 2019) or wind turbines.

DATA AVAILABILITY STATEMENT

The datasets analyzed in this manuscript are not publicly available. Requests to access the datasets should be directed to IM, i.manola@vu.nl.

AUTHOR CONTRIBUTIONS

IM, JS-B, and MB developed the idea for this work. IM and MB analyzed and made the figures. All the authors have contributed in writing the text of this work.

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Avian Reproduction in a Warming World

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Weather influences both the distribution and life-history strategies of birds. Temperature ranks amongst the more important weather parameters in this regard since warming springs in temperate and high latitudes and more frequent heat-waves globally have caused major changes in breeding phenology and negatively affected adult and juvenile survival, respectively. Both long-term and stochastic changes in temperature can have fundamental consequences for avian reproduction even when the effects are not lethal, such as via thermal constraints on parental provisioning and chick growth. To date, most of what we know about temperature effects on nestling development and parental effort during reproduction is based on correlative data. In addition, an increasing amount of evidence indicates that temperature change also significantly affects birds that breed in cooler temperate areas, which so far has been somewhat overlooked. Therefore, in this perspective piece, we outline the existing literature on temperature effects on nestling development and parental behavior, with an emphasis on what needs to be done to address the causal effects of temperature change on avian reproduction under climate change. We finish by providing an outlook over future avenues of research, and give suggestions of some specific areas that might be especially promising in developing this field of research.

Keywords: body temperature, climate change, life history, heterothermy, hyperthermia, overheating, reproduction, trade-off

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INTRODUCTION

Weather and climate have profound effects on the distribution, reproduction, survival and behavior of birds. Two well-known examples are earlier egg laying to track warming springs and increased mortality under extreme weather events. Warmer spring temperatures in temperate and high latitudes have induced phenological shifts to synchronize the start of reproduction with earlier leafing and flowering of plants and the consequently advanced peak of caterpillar abundance (Crick et al., 1997; Visser et al., 1998; Dunn and Winkler, 1999; Sanz, 2002; Charmantier et al., 2008; Källander et al., 2017). Extreme weather events, such as heat waves, occur with increasing frequency around the globe and are predicted to continue to do so (Coumou and Robinson, 2013; Mutiibwa et al., 2015). This has been implicated as a cause of mass mortality events in several taxa, including birds (McKechnie et al., 2012; Fey et al., 2015), and has been suggested to be the driver of the collapse of entire bird communities (Riddell et al., 2019).

All temperature effects are not as apparent and dramatic, but can still influence physiology and behavior with downstream consequences for life-history decisions. Because birds are endothermic and largely homeothermic, they use a suite of behavioral and physiological responses to avoid overheating when air temperature increases. The risk of overheating can be reduced by seeking shade, resting, and drooping the wings (e.g., Smit et al., 2016; Pattinson et al., 2020), which lowers both heat gain and production. When air temperature increases above body temperature, the bird can only lose heat by evaporative cooling. Birds from some orders, such as nightjars and doves, have a substantial evaporative cooling capacity via both cutaneous and respiratory pathways (Smith et al., 2015; McKechnie et al., 2016; O'Connor et al., 2017; Talbot et al., 2017). Other groups, such as songbirds, rely largely on respiratory heat loss through panting, which is less effective and also involves physical work that increases heat production (Whitfield et al., 2015; McKechnie et al., 2017; Smith et al., 2017). Some of the water- and energy costs of high temperatures can be mitigated by a controlled increase in body temperature, "facultative hyperthermia" (e.g., Nilsson et al., 2016; Gerson et al., 2019). This reduces the need for heat dissipation by reducing the thermal gradient between the body and the surroundings, meaning less energy and water is needed to fuel evaporation. While these responses mostly allow the bird to avoid overheating, they are connected to other costs. For example, sustained periods of above-normal body temperature are damaging for cell membranes and may cause oxidative stress (Lin et al., 2006; Daniel et al., 2010; Del Vesco et al., 2015). Moreover, time and energy that is devoted to keeping cool must be procured from other competing demands. It follows that increased investment in thermoregulation could reduce time for other parts of self-maintenance or reproduction in adults, and draw resources away from growth in developing nestlings. Thus, even sub-lethal effects of high temperature are expected to cause population declines through constraints on foraging behavior (Conradie et al., 2019), and higher-than-normal temperature during embryonic or chick development can alter nestling physiology for the duration of the birds' life (reviewed in Nord and Giroud, 2020).

Much of what we know about the adverse effects of high temperature is derived from studies on birds in already hot and dry climates, where additional thermoregulatory challenges to an already challenging life brings effects ranging from devastating to unbearable (McKechnie and Wolf, 2010; Conradie et al., 2019, 2020; Riddell et al., 2019). However, this work is largely correlative, which complicates interpretation of the causal role of changing air temperature in explaining the observed effects. By comparison, we still know relatively little about how increasing temperature and heat waves affect physiology and behavior in adults and chicks in cooler parts of the world. Slight increases in temperature in such biomes could prove beneficial in situations where chick growth is thermally constrained (see below). On the other hand, it is also conceivable that heat waves could have serious consequences since there has likely been, at most, weak selection for heat dissipation and tolerance in temperate regions. Hence, it is clear that we have yet to understand many aspects of the causal effects of air temperature on nestling development and parental effort.

In this perspective paper, we outline the available evidence for heat wave- and temperature change effects and discuss these findings in light of ongoing climate change. We will emphasize that experimental studies are currently in high demand if we are to understand the causality of how future thermal challenges may alter breeding investment and, hence, the trade-off between current and future reproduction. We finish by outlining a number of research trajectories that we believe are the most urgent to address in future work. We will focus on studies on wild birds since those are more likely to be immediately affected by climate change compared to production animals inside temperature-controlled facilities (but see e.g., Naga Raja Kumari and Narendra Nath, 2018). Furthermore, analogous effects in poultry are covered in detail elsewhere (Yahav, 2009; Loyau et al., 2015; Nord and Giroud, 2020).

EFFECTS OF NATURAL VARIATION IN TEMPERATURE ON NESTLINGS

There is substantial variation in the reported effects of temperature on nestling growth and thermoregulation. Much of this variation can probably be explained by geographical location. For example, high air temperatures in already warm and arid parts of the world negatively influence body mass (Murphy, 1985; Cunningham et al., 2013; Salaberria et al., 2014), structural size (Cunningham et al., 2013; Salaberria et al., 2014), nestling mortality (Murphy, 1985), fledging success (Cunningham et al., 2013), and post-fledging survival (Greño et al., 2008). In contrast, high air temperatures in cooler temperate areas can have positive impact on nestling growth (McCarty and Winkler, 1999; Eeva et al., 2002). Other studies have found that nestling growth benefits from stable nest temperatures, but that variable or too high nest temperatures adversely affects growth (Lloyd and Martin, 2004; Larson et al., 2015) and fledging success (Ardia, 2013; Larson et al., 2015). However, air or nest temperature alone is probably inherently correlated with variation in food availability and, hence, parental effort. Although path analysis may aid in separation of direct and indirect effects of temperature (see McCarty and Winkler, 1999; van de Ven et al., 2020) we still need studies that experimentally manipulate nest temperature to unambiguously evaluate the causal role of increasing temperature from environmentally driven effects on parental effort and provisioning.

EFFECTS OF MANIPULATION OF NEST TEMPERATURE ON NESTLING GROWTH AND THERMOREGULATION

Surprisingly few studies have experimentally manipulated nest temperature after hatching, and those that have done so were all conducted at relatively high latitudes. Rodríguez and Barba (2016a,b) found that both increased and decreased nest temperature had negative effects on the growth of great tit (*Parus major*) nestlings in a Mediterranean habitat and that heated nestlings suffered reduced post-fledging survival (Rodríguez et al., 2016). This suggests that natural nest temperature was close to optimal for nestling development. In contrast, Dawson et al. (2005) found that moderate heating of tree swallow (*Tachycineta bicolor*) nests increased both nestling growth and fledging success in a northern, temperate area. These studies did not record changes in nestling body temperature or any other metabolic responses to the manipulation. Thus, we do not know if the effects of changing temperature can be explained by alteration of the ontogeny of thermoregulation in the nestlings. Andreasson et al. (2018) heated blue tit (*Cyanistes caeruleus*) nests and measured both nestling growth and thermoregulatory responses to the manipulation. These authors found that nestlings in heated nests had a higher body temperature and lower body mass gain throughout the nestling period. Body temperature was high and stable in the heated group even at developmental stages where the control birds were poikilothermic. Hence, it is conceivable that the suppressing effects on growth were, at least partly, explained by increased allocation of resources to thermoregulation. Yet, Andreasson et al. (2018) found no effects on mortality in the nest and, surprisingly, reported slightly higher apparent long-term survival in heated nestlings.

EFFECTS OF TEMPERATURE ON PARENTAL FORAGING AND EFFORT

In already hot and dry environments, high air temperatures commonly result in reduced foraging rate, mostly due to increased resting during the hottest parts of the day (Tieleman and Williams, 2002; Edwards et al., 2015; Funghi et al., 2019). In addition, foraging success also declines with increasing air temperature, either due to difficulties in combining foraging with behaviors promoting heat dissipation (du Plessis et al., 2012) or due to reduced food availability when prey seek shelter from high temperatures (Cunningham et al., 2013). Hence, nestlings will be fed less, and with lower quality prey, when temperatures increases (Cunningham et al., 2013; Wiley and Ridley, 2016), resulting in costs to growth (Cunningham et al., 2013). It follows that continuing climate change may exacerbate current constraints on foraging to a point where the distribution of bird species in hot and arid areas will be severely restricted, not only due to lethal effects of overheating but also due to missed opportunities that could otherwise have been used for reproduction (Conradie et al., 2019). This could explain why some desert birds with long potential breeding seasons increasingly avoid breeding during the hottest parts of the year (Duursma et al., 2017). Cooperative breeding is commonly observed in such biomes, which is typically interpreted as a mechanism to ameliorate the effects of challenging and unpredictable environments (Rubenstein and Lovette, 2007). It follows that increasingly challenging thermal environments might trigger changes to the size and genetic make-up of cooperative breeder groups as a means of minimizing negative effects on nestlings. However, although high mean daily maximum temperatures reduced nestling survival in southern pied babblers (*Turdoides bicolor*), larger group sizes of feeding adults could not buffer this effect (Bourne et al., 2020a).

We argue that constraints on foraging success and provisioning rate due to high air temperature are not just confined to hot and arid areas, since, just as in hot environments (Nilsson et al., 2016), adults in temperate areas show increasing body temperature at higher air temperature (Nilsson and Nord, 2018). On top of this, experimental work has shown that body temperature increases with increasing parental effort, resulting in heat storage (Nilsson and Nord, 2018). If parents cannot dissipate this excess heat at the same rate as it is produced, they may reach a point where they have to reduce work rate to avoid the deleterious consequences of sustained hyperthermia (Speakman and Król, 2010). For example, breeding starlings (*Sturnus vulgaris*) reduce provisioning rate when air temperature increase, probably due to increased heat load (Clark, 1987). It follows that the risk of hyperthermia due to increased heat load may shift the diurnal pattern of nestling feeding. By concentrating feeding to cooler times of the day, i.e., dusk and dawn, the risk of hyperthermia might be minimized given that nestlings can sustain the resultant longer periods of low provisioning rates. The risk of overheating may also affect birds during other parts of the annual cycle. Eider ducks (*Somateria mollissima*) in the Baltic Sea stop flying altogether when reaching a heat storage threshold (Guillemette et al., 2016).

EVALUATING THE CAUSAL ROLE OF TEMPERATURE ON PARENTAL EFFORT

While it is difficult to manipulate air temperature in natural environments, some studies have increased parents' ability for heat dissipation by removing the feathers covering the ventral parts of the body to create a thermal window. After experimental facilitation of heat dissipation, nestling-feeding blue tits in northern Europe could maintain work rate whilst simultaneously reducing body temperature, investing more in self-maintenance, and siring larger nestlings (Nord and Nilsson, 2019). Feather-clipped female tree swallows at a temperate site in North America had higher feeding rates (at least in hot air temperatures) and produced heavier nestlings compared to controls (Tapper et al., 2020). This underlines that effects of high temperatures are likely also in temperate areas. However, the effect of a release from the risk of overheating may be context-dependent. For example, in another study on blue tits, breeding females used the reduced constraints on foraging effort to invest in self-maintenance by increasing their level of constitutive innate immunity (Andreasson et al., 2020).

THE LINK BETWEEN TEMPERATURE, PARENTAL EFFORT AND NESTLING PHENOTYPE

Reduced and variable provisioning rates in higher-than-normal temperatures may put nestlings into periods of food stress. This can cause irreversible effects on the subsequent adult phenotype (e.g., Monaghan, 2008). For example, zebra finch (*Taeniopygia guttata*) nestlings reared under food restriction had higher intake rates and basal metabolic rate in adulthood than nestlings reared with *ad libitum* food (Careau et al., 2014). Furthermore, zebra finch nestlings in the wild fledged at smaller size in warmer than in somewhat cooler areas (Andrew et al., 2017). This size difference remained when zebra finches were reared in captivity with *ad libitum* food (Andrew et al., 2017). This indicates that body size changes may be a result of either thermal adaptation to reduce heat load, or a direct suppressing effect of heat on nestling growth (Andreasson et al., 2018), more than a consequence of altered parental behavior *per se* (Wiley and Ridley, 2016). Thus, increasing temperatures during nestling development can drive changes in physiological and morphological traits that remain to adulthood in both direct and indirect ways (see also Nord and Giroud, 2020).

FUTURE PERSPECTIVES

The few studies on heat constraints on avian reproduction that are available from colder parts of the world suggest that, just as in hot and dry areas, higher-than-normal temperature can suppress current and future reproduction in both direct and indirect ways. However, most causal aspects of thermal constraints on parental effort and chick development remain largely unexplored. It will be particularly important to separate the causal role of temperature on adult and juvenile traits from any associated, indirect, effect of temperature on the ecosystem. Below, we outline what we believe to be the most critical areas for future investigation and experimentation, with the hope of catalyzing further and broader study within this timely research field.

(i) *Broader geographic and environmental coverage:* Previous studies suggest variation in effects of heat exposure depending on the thermal context of the habitat. There is now a need to broaden the latitudinal and altitudinal coverage to better understand when increasing temperature is ameliorating and when it is constraining. Studies should also assess when, within a site, a given temperature change transitions from being beneficial to detrimental, and how this varies across a species' range, which could indicate potential for local adaptation.

(ii) *Experimental studies:* With few exceptions, studies that have investigated the thermal sensitivity of bird reproduction have used natural variation in air or nest temperature, which limits conclusions on causality. We need more studies that manipulate the thermal environmental or heat transfer processes in parents and/or chicks in fully factorial designs within and beyond predictions from climate change models in both cold and warm locations (e.g., IPCC, 2013; **Figure 1**). This will inform us about the extent to which climate change and extreme weather events may impact life history trade-offs. Likewise, there is a need for studies that heat-challenge parents in the wild, because the current approach of relieving constraints need not be ideal to reveal reproductive trade-offs, since: (1) the experimental effect is opposite to that experienced during a heat wave and (2) parents may re-allocate saved resources through different pathways depending on individual demands (e.g., Andreasson et al., 2020). Possible avenues for achieving this could include increased flight costs, changes to lipid content/composition of the skin or other changes to body insulation to alter thermal conductivity, and pharmaceutical treatment to induce peripheral vasoconstriction with consequent reduction in dry- and respiratory heat loss. These methods are not without problems since they inevitably will influence other physiological processes and/or aerodynamic performance of the bird.

(iii) *A physiological perspective on behavior:* Studies addressing the constraining role of air temperature on avian reproduction would gain from increasingly incorporating thermo-physiological measurement. Because temperature-effects on nestling development and physiology can be expected to be quadratic, with adverse effects occurring at the warm and cold end of the spectra, such measurements will provide crucial mechanistic depth to observed fitness consequences, such as why heat stress during development sometimes improve short- or long-term survival (Dawson et al., 2005; Andreasson et al., 2018) but at other times negatively affect survival (Rodríguez et al., 2016).

(iv) *Studies across life histories:* It is conceivable that species with different life histories, e.g., slow- or fast-paces of life or resident vs. migratory behavior, will be differentially affected by temperature change. For example, species with lower work rate, long lifespan and small brood sizes may be better equipped to deal with heat waves, e.g., by reducing reproductive effort during heat wave years (cf. Martin and Mouton, 2020). Moreover, most birds at high latitudes are migrants (Newton and Dale, 1996). At least in some cases, such birds have not advanced the start of reproduction to match warming springs when resident, sympatrically breeding, species have (e.g., Källander et al., 2017). Thus, there may be selection for residency, increasing the proportion of residents in partially migratory birds. In addition, it remains to be tested if the decreased activity during the hottest part of the day, commonly observed in warm and dry areas (Tieleman and Williams, 2002; Edwards et al., 2015; Funghi et al., 2019), will become more pronounced with increasing temperatures globally, and more common overall in temperate biomes.

(v) *Short- and long-term effects on the individual:* In some cases, a high temperature during breeding is conducive for growth and survival (Dawson et al., 2005). In other cases, higher temperature appears constraining in the short term, but beneficial for fitness over longer time periods (Andreasson et al., 2018). In other cases still, it may be the other way around (Nord and Nilsson, 2016). Future studies should monitor fitness effects of temperature over the life span of an individual, and ideally couple this to measurements of physiological mediators of the observed effects.

(vi) *Population-level effects:* Reports on temperature-driven breeding failure (e.g., Sharpe et al., 2019) or altogether

FIGURE 1 | Putative designs for manipulation of heat transfer in nestlings and adults. There is a need for more experimental studies to address the causality of temperature effects on avian reproduction in a warming world. **(A)** The thermal environment of the nest, at least for hole-nesting species, can easily be manipulated by the addition of a chemical (e.g., hand warmers, as in the figure) or an electrical heating device below the nest. **(B)** Parental heat transfer can be manipulated by removal of the plumage covering the abdomen and pectoral muscles (the main heat-producing tissue) using small scissors. Future studies should also seek to device methods to *decrease* heat transfer rate in parents. Photographs © Jennifer Page [University of Glasgow; Panel **(A)**], Andreas Nord **(B)**.

skipped breeding seasons (e.g., Duursma et al., 2017; see also Martin and Mouton (2020) for similar effects in relation to drought periods) are becoming increasingly frequent. If this occurs in short-lived species that are unlikely to reproduce more than once, or if coupled to mass mortality events (McKechnie and Wolf, 2010; Riddell et al., 2019), population-level effects are expected. It would be interesting to know e.g., how selection for temperature tolerance operates and manifests under such circumstances (cf. Burggren, 2018; Stillman, 2019), and whether there is compensatory breeding in long-lived species in the breeding season following an extreme weather event (sensu Bourne et al., 2020b) also in temperate areas.

(vii) *Heritability of temperature-induced effects:* Studies on wild and domesticated animals show that key thermoregulatory traits, such as heat production, body temperature, and temperature tolerance, show moderate to high heritability (typically 0.4–0.6) (e.g., Bowen and Washburn, 1984; Ueno and Komiyama, 1987; Nilsson et al., 2009). It is relevant to ask if induced non-genetic changes to the thermoregulatory phenotype are also inherited. For example, if offspring to parents that developed during, or later experienced, a heat wave are born "heat tolerant," they might be maladapted to the normally colder temperatures of their habitat. Work on ectotherms (e.g., Wang et al., 2015) and plants (e.g., Li and Brawley, 2003) show that parents exposed to warm temperature sire offspring that are more heat-tolerant. To the best of our knowledge, there are no corresponding data for endotherms.

CONCLUSION

It is clear that increasing global temperature and frequency of extreme weather events may reduce work rate with consequences for parental effort in both warm and, notably, also in temperate environments. This can add to direct, negative effects of high temperature on juvenile growth and maturation (Nord and Giroud, 2020). In hot environments, these factors may result in a shift in the timing of breeding (Duursma et al., 2017), or even aborted breeding (e.g., Sharpe et al., 2019), ultimately causing a shift in distribution ranges (Conradie et al., 2019). In temperate areas, the consequence of reduced work rates may be smaller brood sizes and general changes of life history strategies (Nilsson and Nord, 2018).

Future adaptations to a warmer climate at temperate latitudes may parallel extant adaptations to hot environments, e.g., reduced metabolic rates (Wiersma et al., 2007a,b) to reduce baseline heat production, and reduced reproductive investment (Cardillo, 2002; Wiley and Ridley, 2016) to reduce work rate (and, hence, the amount of activity-generated heat). We also speculate that temperate species may shift their main activity to cooler times of the day, as is known for hard-working, breeding rodents (van der Vinne et al., 2014). Such small mammals have been predicted to become increasingly nocturnal in a warmer world

(Bonebrake et al., 2020). This is already the strategy chosen by most bats, possibly to avoid adding solar heating to an already heat-generating life style (Speakman et al., 1994). It is unlikely that presently diurnal birds will evolve a nocturnal way of life on account of constraints on foraging in the dark. However, in the future, a greater part of the active foraging time may be allocated to dusk and dawn with a consequent potential increase in mortality by aerial predators.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article.

AUTHOR CONTRIBUTIONS

AN conceived the idea. All authors devised the structure of the manuscript, wrote and edited the manuscript, approved the final version, and agreed to be accountable for all contents.

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Location Is Everything, but Climate Gets a Share: Analyzing Small-Scale Environmental Influences on Breeding Success in the White-Throated Dipper

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Ecological and evolutionary effects of environmental variation on wild populations are of particular interest in a changing world. Large-scale environmental indices are classically used as environmental explanatory variables to study climate change effects on wild populations. However, these measures neglect the fact that individuals are affected by the local conditions in their home ranges. Freshwater ecosystems are particularly sensitive to climate change induced alterations in precipitation and discharge affecting lower trophic level prey and cascading up the food chain to impact keystone species. Here, we study how small-scale environmental variation at the level of each territory affects fitness-related traits and in particular reproductive success in the white-throated dipper *Cinclus cinclus*, a bird dependent on aquatic prey. We take advantage of a long-term study of breeding dippers in a natural river system in Norway (1978–2015). We relate daily river discharge and other important hydrological and territory location variables to clutch and brood size simultaneously, while accounting for male and female age, polygyny, and population density. We also address uncertainty in estimates of both clutch and brood size when modeling reproductive success. The most influential variable overall was the altitudinal gradient, where birds breeding at higher altitudes laid fewer eggs and fledged fewer young. Clutch size decreased with increased population density and high temperatures, while it was positively affected by female age. Brood size varied greatly among territories, where some territories had consistently larger broods than others. Increased minimum and maximum temperatures, river discharge above 10 l/s and increased variability in snow depth had a positive effect on brood size, whereas polygyny had a negative effect. In conclusion, territory-specific variables explained a large amount of the variation in the reproductive output in the dipper, emphasizing the importance of the local habitat, and not only climatic variation, in a keystone species in freshwater ecosystems.

Keywords: brood size, *Cinclus cinclus*, clutch size, habitat quality, hydrology, polygamy, treating uncertainty

INTRODUCTION

Understanding how environmental fluctuations affect individual fitness is central in ecology and evolution. Freshwater ecosystems are particularly sensitive to climate change-induced alterations in precipitation and river discharge (Hanssen-Bauer, 2005). Indeed, extreme fluctuations in river discharge cause disturbances in aquatic food webs, including lower trophic level-prey. These disturbances may also cascade up the food chain and negatively affect the reproductive success of higher trophic levels. Also, shifts in timing of droughts and river flooding events might directly reduce reproductive opportunities for species that strongly depend on water to reproduce, such as waterbirds (Chiu et al., 2008; Royan et al., 2013).

Large scale climate indices such as the North Atlantic Oscillation (NAO) are often assumed to represent an environment experienced by all population members (Sæther et al., 2000; Frederiksen et al., 2008; Nilsson et al., 2011a; Gamelon et al., 2017). However, even on a population scale, the environment is rarely uniform (Cole et al., 2015; Hinks et al., 2015), and such indices are unlikely to accurately capture the environmental conditions at the most biologically relevant scale (Mauck et al., 2018). Individuals in a population are rarely roaming the entire population space, particularly not territorial species. Thus, focusing on the scale at which the environment is interacting with the individual is key to understand the causes and consequences of ecological and evolutionary processes on individual fitness, and is an area where we commonly are hampered by a lack of small-scale environmental measurements (Nilsson et al., 2011b; Cole et al., 2015).

Understanding how environmental variation affect individual fitness requires accurate estimates of fitness-related traits in the studied population. For instance, in birds, recording the number of eggs in a clutch (clutch size) when the eggs have already hatched seems straightforward enough; there simply must have been at least as many eggs as nestlings (brood size). Thus, brood size obviously depends on clutch size. However, assuming that the brood size accurately represents the initial reproductive effort of a female may often be an underestimated source of uncertainty (eggs or nestlings may be lost before the nests are visited, eggs could be unfertilized or not hatched by other reasons). Also recording the number of nestlings when the brood rapidly is approaching fledging (leaving the nest) is also associated with uncertainty. For instance, there could be one or more offspring already having left the nest, or in worst case, the field observer might not encounter the nest until after fledging where there might be obvious signs of the brood having successfully fledged but the number of fledglings is unknown. Accounting for uncertainty when estimating fitness-related traits is fundamental in science (Fischhoff and Davis, 2014). If uncertainty is not accounted for, this can lead to serious errors during model selection in regression analyses and thus lead to misleading hypothesis testing. In this study, we acknowledge the fact that clutch and brood size are not independent variables, and we furthermore address the uncertainty in the estimates of both clutch and brood size when modeling breeding success in a study system where uncertainty has been recorded since the start of the study in 1978 (Nilsson et al., 2019).

Here, we focus on the effects of local environmental conditions at the territory scale (i.e., multiple hydrological variables at each territory, and model-input derived from a 1 × 1 km meteorological grid; Skaugen et al., 2015) on reproductive success in the white-throated dipper *Cinclus cinclus* (hereafter dipper), taking advantage of a long-term monitoring program (1978–2015; Nilsson et al., 2011a). The dipper is a passerine bird with an obligate aquatic lifestyle. Previous work has shown that the species population dynamics responds to variation in winter climate and spring phenology, responding to warmer springs but also to variation in territory quality (Nilsson et al., 2011a, 2019; Gamelon et al., 2017, 2018). However, the documented effects of regional temperatures and precipitation, ice conditions on the major lake in the study area, and NAO, are most likely extrapolations of microclimatic conditions, such as local river discharge and temperature, snow conditions within the territories, which we previously have had no information on. Based on the model, and the model input variables derived from a small-scale meteorological grid, we could use a number of accurate estimates of local environmental variables and relate these to reproductive success. Given the effect of future climate predictions on population dynamics (Gamelon et al., 2017), attributing reproductive success to variation in specific local variables is of particular interest. The lower parts of the river system have been limed to mitigate the effects of acidic precipitation, because such acidification has negative impacts on dipper reproductive performance (Ormerod et al., 1991; Nybø et al., 1997; Nilsson et al., 2018). We therefore also included information on liming status among the explanatory variables. In the present study, while assessing the effect of local environmental conditions on reproductive output, we have also taken male and female age, polygyny and population density into account. In addition to shedding light on the variables that are most important for breeding success, this exercise led us to draw some general conclusions about statistical modeling of biological systems, which deserves more attention.

MATERIALS AND METHODS

Study Species and Study System

The dipper is a medium-sized passerine bird (50–70 g) distributed across mountainous areas in the Palearctic. It feeds on submerged aquatic invertebrates and fish in running clear freshwater (Ormerod et al., 1987; Tyler and Ormerod, 1994). Breeding is restricted to the immediate vicinity of fast-flowing rapids, where the nest is situated so that the opening is almost always placed immediately above fast-flowing water. Dippers lay approximately 5 eggs and start incubation after the clutch is completed. The female incubates for approximately 17 days and the young remain in the nest for about 22 days (Borgström, 1991). The Scandinavian dipper population is partially migratory, meaning that part of the population undertakes migration while the remaining birds winter on or close to the breeding grounds (Terrill and Able, 1988). Norwegian migratory dippers are recovered mainly in Denmark, Sweden, Northern Germany, and Poland (Bakken et al., 2006).

The study population is located in the river Lyngdalselva in southernmost Norway (**Figure 1**; 58°08′–58°40′N, 6°56′–7°20′E). The dipper population has been studied since 1978 following a standardized monitoring program (see Nilsson et al., 2011a for details). There is a strong altitudinal gradient in the study river system, from the outlet into the sea up to 700 m above sea level, in addition to a coastal-inland gradient reaching 60 km inland (**Figure 1**). The population size fluctuates between years with a range of 20–117 breeding pairs, typically declining after cold winters and increasing after mild ones (Nilsson et al., 2011a). The total number of recorded breeding events are 2585 by 2165 breeding females.

Dippers defend territories, which contain one or more appropriate nest sites. Because the dipper has such particular nest site requirements (see above), the number of territories in our study system is limited to 158. Some territories are almost always occupied, while others have only been in use for a single year. The downstream and upstream boundaries of a territory might vary slightly between years, particularly depending on whether the neighboring territories are occupied or not, but the major part of a territory remains constant between years (Nilsson et al., 2019).

All known territories in the river system were visited in the early morning hours during the nest building phase and scanned for dipper activity. Breeding was defined as positive when inner nest building was completed. Dippers build an outer and an inner nest, where the outer nest can be used year after year. The inner nest is rebuilt each year and both sexes participate. At first encounter, adults were caught and ringed with an aluminum ring and given an individual color code in the form of two plastic color rings. Adult birds were accurately aged and sexed according to Svensson (1992). The clutch and brood sizes of almost all occupied nests are thus known and nearly all young were ringed with an aluminum ring. Clutch size was recorded during incubation, and brood size was recorded when the young were ringed in the nest. Uncertainty in the exact clutch and brood size was recorded when appropriate. Uncertainty can be caused by the disappearance of eggs, re-laid clutches, variation in chick survival and food provisioning, or when the nest is inaccessible and requires aid from mountain climbers, etc.

The mating system in the dipper is primarily monogamous, but occasionally polygynous. The prevalence of polygyny varies between populations (Wilson, 1996). Polygynous males occupy two or more territories with one female in each territory. In our area, assessing the mating system is complicated by the fact that occasionally females might sequentially make several breeding attempts with different males, often when the first breeding attempt fail. In some instances, females have even been observed to build nests at two different territories with two different males. However, the female only lays eggs in one of the built nests. We termed this mating strategy sequential monogamy. Polyandry is defined as multiple mating where the female's clutch is fertilized by more than one male (Parker and Birkhead, 2013), but we have no observations of females actually mating with both males. The incidence of extra-pair young seems generally very low in the dipper, only 2% in another river in Norway (Øigarden and Linløkken, 2010).

Hydrology and Small-Scale Data

Hydrology data are usually obtained from gauged sites, but in Lyngdalselva only two sites are gauged. Therefore, hydrology data in this study is based on predictions in ungauged basins, at each dipper breeding territory (145 of 158 territories; the remaining territories had too small catchments to allow predictions) using the rainfall-runoff model (the Distance Distribution Dynamics (DDD) model; Skaugen et al., 2015). Digitized maps of terrain and river networks form the basis for estimations of many of the DDD model parameters. For the study period 1978–2015, daily river discharge data have been estimated, in addition to snow covered area (SCA), snow water equivalent (SWE) and groundwater levels. The model for Lyngdalselva is extremely good when comparing model predictions and gauged sites; the Kling Gupta Efficiency criterion (KGE; Gupta et al., 2009; Kling et al., 2012) for both gauged sites in Lyngdalselva is 0.94. Thiemig et al. (2013) regard values KGE 0.5–0.75 as intermediate, and 0.75–0.9 as good; a KGE of 0.94 for Lyngdalselva is thus very good.

River discharge can be of vastly different magnitudes in different territories. Mean discharge in territories in mountainous brooks can be as small as 0.008 m^3/s, while river discharge at the last territory before the outlet into the sea is 32 m^3/s. To allow comparison between territories with large differences in discharge, we standardized river discharge with two methods: (1) as the relative river discharge (defined as discharge divided by the territory mean discharge for the study period), and (2) as specific discharge, that is discharge per area, measured in $l/s/km^2$, in each breeding territory.

To determine during which time periods different environmental variables would affect the dippers' reproductive success, we defined an annual trigger date for each territory (**Supplementary Material 1**). Whether the river is ice-covered or not, is of vital importance for the dipper and initiation of

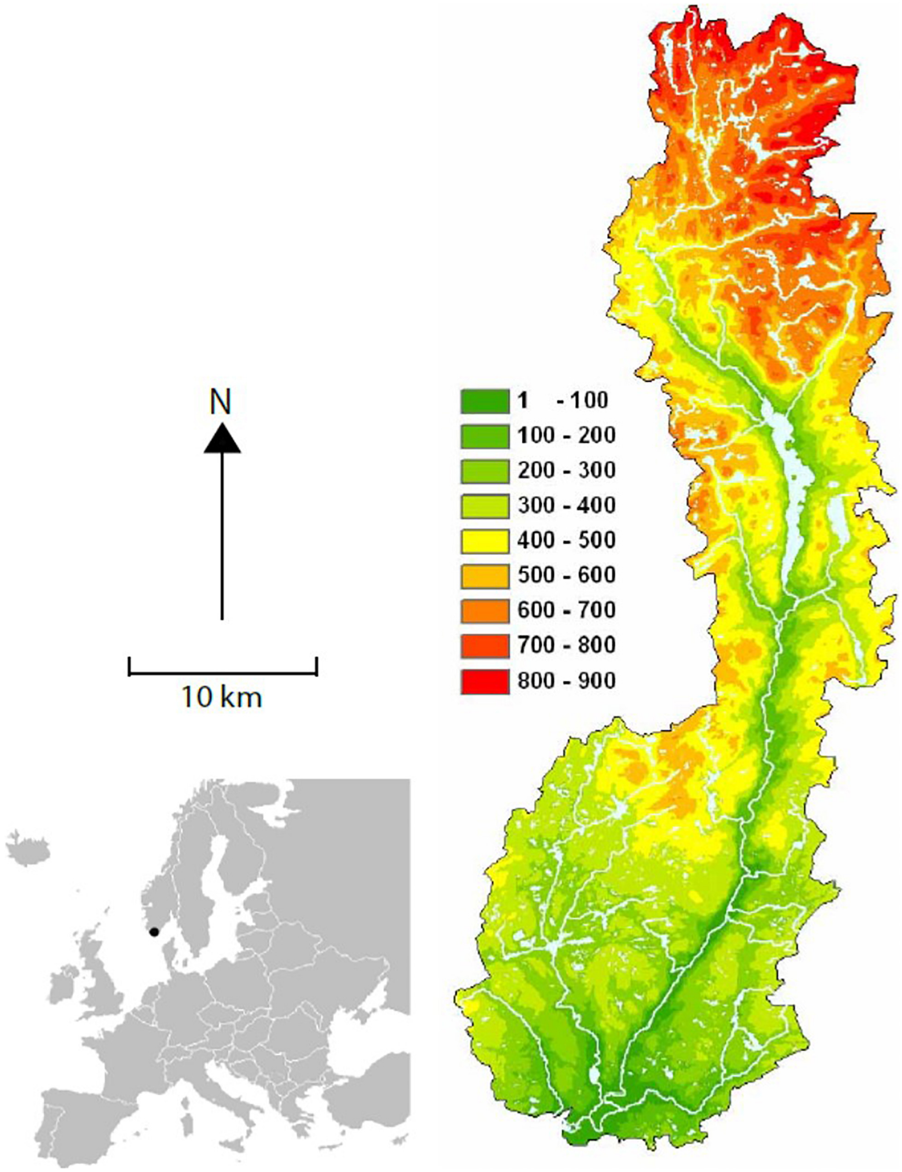

FIGURE 1 | Map showing the altitudinal gradient (m) in the Lygna watershed.

breeding, because dippers find all of their food under water. We therefore defined the annual trigger date as the first date when the daily air temperature exceeded 0°C for five consecutive days after 1st of February. Based on the trigger date we defined a number of different time periods, defined as trigger periods, with different starting dates and of different durations, in addition to a number of statistically defined periods. For a full description of trigger dates and trigger periods, see **Supplementary Material 1**.

Statistical Analyses

The data included 2585 breeding events, where 1177 (45.4%) had a definitive recorded clutch size (no uncertainty). Among the recorded brood sizes, 2474 (95.7%) were definite brood sizes (no uncertainty).

Breeding Success Model

If the exact number of eggs (clutch size) and chicks (brood size) were known, the probability of an egg hatching, i.e., the probability of a chick from an egg given the fixed effects could be modeling using standard General Linear Model (GLM) regression. However, for some of the observed breeding events, there was considerable uncertainty in the exact clutch and/or brood sizes and this uncertainty must be taken into account when analyzing the effects of the explanatory variables. We addressed this by using the likelihood expression for the mentioned GLM model but sum over the set of possible eggs and chicks. This likelihood expression mixes the regression coefficients for the number of eggs and chicks, thus the task of doing regression on eggs and chicks is no longer two separate tasks but must be made in one larger analysis. Typical binomial GLM models use logit(probability) = linear combinations of explanatory variables, and logit(probability) is equivalent to log(odds), where odds = probability/(1 − probability); Thus the effect of a change in each explanatory variable can most readily be interpreted as a change in the odds, and we will thus discuss the results in this manner. For more details on the statistical modeling, such as how we handle random factors and per measurement variation, see the **Supplementary Material 2**.

Selection of Explanatory Variables

In addition to the hydrology and other deducted variables such as local temperature, precipitation, and catchment area size, from the work by Skaugen et al. (2015), we included altitude, distance from the coast, male and female age and identity, and polygyny status, as possible explanatory variables of breeding success in the dipper. A full list of the examined possible explanatory variables is available in **Supplementary Table S2.1**. The total number of possible explanatory variables examined were 109, among which 101 were continuous fixed effects, two were categorical fixed effects, and six were random effects.

The set of possible explanatory variables was explored in a step-wise-up manner, by starting with a model without any explanatory variables and for each iteration examining all models where each explanatory variable not already included is added to the explanation variables already included. Bayesian model likelihood (BML) was used to evaluate each model. The procedure stopped at the iteration where none of the new models examined was (statistically) significantly better than the best model from the previous iteration, see the **Supplementary Material 2** for more information on how we explore the model space as well as for a description of the Markov Chain Monte Carlo (MCMC) algorithm used and the BML.

Sequential Monogamy

In the initial stages of modeling breeding success, sequential monogamy was a major contributor to explain variation in brood size. However, in sequential monogamy, the first breeding attempts usually failed (62.5%). After correcting for the natural sequence of events in sequential monogamy, sequential monogamy was excluded from among the variables contributing to explaining variation in breeding success. However, because of this instance, we decided to investigate this behavior further. Consequently, we first summarized the individual number of total breeding events and the number of sequentially monogamous breeding events, for each female. This enabled us to test for over-dispersion (binomial vs. beta-binomial model), in order to test whether there are females with a penchant for the behavior or whether it occurs randomly. After that, we examined sequential monogamy per breeding event as the response in a General Linear Model (GLM) model (binomial response), using a Bayesian Information Criterion (BIC)-based stepwise search. Lastly, we assessed whether the behavior could be an indicator of inherent, unmeasured female quality and how this would affect reproductive success. Thus, we created a new indicator variable for whether the female at any point in her history had had a sequentially monogamous breeding event. We added this new indicator variable to our resulting model for breeding success (egg and/or chick probability). If one of these extra models had a better Bayesian model probability, i.e., if sequential monogamous history could explain some of the reproductive success even when correcting for whether or not each particular breeding event was sequentially monogamous, then the history of that behavior as an indicator of inherent female quality would hold true.

RESULTS

Breeding Success Model

The breeding success model resulted in the following effects: altitude (eggs and chicks), a temporal trend (eggs), territory id (chicks), population size (eggs), female age (eggs), temperature maximums from the trigger date and until 9 days after (eggs) and temperature minimums 10 days centered on the trigger date (chicks), polygyny (chicks), temperature maximums last autumn (chicks), the quadratic distance to the coast (eggs), when the discharge decreased below 10 l/s 35–50 days before the trigger date (chicks), the variation in snow depth (SWE) 20–5 days before the trigger date (chicks), the variation in the discharge from the trigger date and until 9 days after (eggs), etc. (for a full list, see **Tables 1**, **2**), where the effects are ordered as they were found by the step-wise search (**Tables 1,2**; for interpretation of regression coefficients, see Eqs. (2) and (4) in the **Supplementary Material 2**).

The strongest fixed effect was altitude for both the number of eggs and chicks (**Tables 1**, **2**). The odds for producing an egg went down by a multiplicative factor of 0.84 for each 100 m higher up the territory was, that means that the odds were reduced by 16% for each extra 100 m of altitude. Similarly, the odds for producing a chick from each egg were reduced by a multiplicative factor of 0.83, i.e., a reduction of 17% per 100 m of extra altitude (**Figure 2A**). The odds for hatching success (effect on number of eggs times effect on number of chicks) was overall more than 12 times as high at sea level as it was at the territories at 700 m asl (**Figure 2B**). These were huge effects, highlighting the importance of the altitudinal gradient for breeding success.

The regression estimate for territory identity as a random factor for the number of chicks means that the odds can vary with a multiplicative factor ranging with 95% probability between 0.50 and 2.00. In essence, territory can halve or double the odds for chicks. This implies that some territories consistently produced larger clutches than expected, while other territories produced much smaller clutches. The odds for producing an egg increased by 12% per decade (**Figure 2C**), by 6.4% for each extra year the female ages, and by 7.9% when the distance to the coast went from 0 to the median value of 23.3 km (however, this was a quadratic effect). The odds for producing chicks decreased by 5.9% for an increase in population size of 10 new individuals (**Figure 2D**), decreased by 24% if the male was polygynous and increased 41% if the indicator for low discharge was set (which it is if the discharge becomes lower than 10 l/s in the period going from 50 to 35 days before the temperature-driven trigger date).

In summary, the most important model effects on the number of eggs laid were altitude (66.4%), distance from the

TABLE 1 | Parameter estimates for a model explaining white-throated dipper clutch size in River Lyngdalselva 1978–2015 (see Eqs. (2) and (4) for interpretation, **Supplementary Material 2**).

Effect	Fixed (F) or random (R) factor	Estimate	95% credibility band	Variance contribution	Variable description
Altitude	F	−0.00168	(−0.00212, −0.00128)	66.4%	Altitude of most frequented nest in territory
Linear time	F	0.0114	(0.0071, 0.0161)	9.0%	Temporal trend
Female age	F	0.0628	(0.0315, 0.0914)	4.7%	Female age
T.max.11	F	−0.0319	(−0.0617, −0.0049)	1.9%	Temperature maximum 0–9 days after trigger date
Distanceˆ2	F	0.000140	(0.000005, 0.000215)	12.7%	Distance from river outlet to most frequented nest in territory
Qnorm.sd.09	F	0.0277	(−0.0168, 0.0724)	0.3%	Variation in normalized discharge -50–35 days before trigger date
T.max.33	F	0.0182	(0.0037, 0.0302)	1.9%	Temperature maximum −15– + 10 days before trigger date
Swe1.sd.11	F	−0.00463	(−0.00862, −0.00069)	2.2%	Variation in snow-water equivalent 0–9 days before trigger date
P.mean.23	F	−0.0300	(−0.0636, 0.0070)	1.0%	Mean precipitation previous April 1st–August 31st
P.mean.22	F	0.0223	(−0.0093, 0.0561)	Pooled with P.mean.23.	Mean precipitation previous April 1st–June 1st

Effects sorted by order of discovery. Variance contribution of fixed effects were estimated using standardized regression coefficients.

TABLE 2 | Parameter estimates for a model explaining white-throated dipper brood size in River Lyngdalselva 1978–2015 (see Eqs. (2) and (4) for interpretation, **Supplementary Material 2**).

Effect	Fixed (F) or random (R) factor	Estimate	95% credibility band	Variance contribution	Variable description
Altitude	F	−0.00186	(−0.00242, −0.00128)	36.3%	Altitude of most frequented nest in territory
Location	R	0.354	(0.240, 0.475)	39.6%	Territory identity
Population	F	−0.00607	(−0.00883, −0.00343)	8.8%	Population density
T.min.4	F	0.0268	(0.006, 0.0471)	2.9%	Temperature minimum −5– + 4 days before trigger date
Polygyny	F	−0.276	(−0.472, −0.087)	3.2%	Polygyny indicator (0 = no, 1 = yes)
T.max.20	F	0.0361	(−0.011, 0.0741)	1.3%	Temperature maximum previous September 1st–November 30th
Qlt10.09	F	0.341	(0.111, 0.595)	3.7%	Indicating whether discharge exceeded 10 l/s –50–35 days before trigger date (0 = no, 1 = yes)
Swe1.sd.02	F	0.0104	(0.0020, 0.0192)	2.7%	Variation in snow-water equivalent –20–5 before trigger date
P.mean.22	F	0.0321	(−0.0119, 0.0765)	0.4%	Mean precipitation previous April 1st–June 1st
Male age	F	−0.0269	(−0.0567, −0.0012)	0.4%	Male age
NAO.11	F	0.0440	(−0.0297, 0.1252)	0.2%	North Atlantic Oscillation 0– + 9 days after trigger date
Qnorm.sd.09	F	0.0176	(−0.0387, 0.0730)	0.05%	Variation in normalized discharge –50–35 days before trigger date
Qnorm.mean.46	F	−0.0652	(−0.1814, 0.0575)	0.4%	Mean normalized discharge 21−31 days after predicted hatching day.

Effects sorted by order of discovery. Variance contribution of fixed effects were estimated using standardized regression coefficients.

coast (12.7%), the temporal trend (9.0%), female age (4.7%), temperature (3.8%) and snow (2.2%), while the most important model effects on number of chicks were altitude (36.3%) and territory identity (39.6%), followed by population size (8.8%), temperature (4.2%), discharge (4.2%), polygyny (3.2%) and snow (2.7%) (**Tables 1**, **2**).

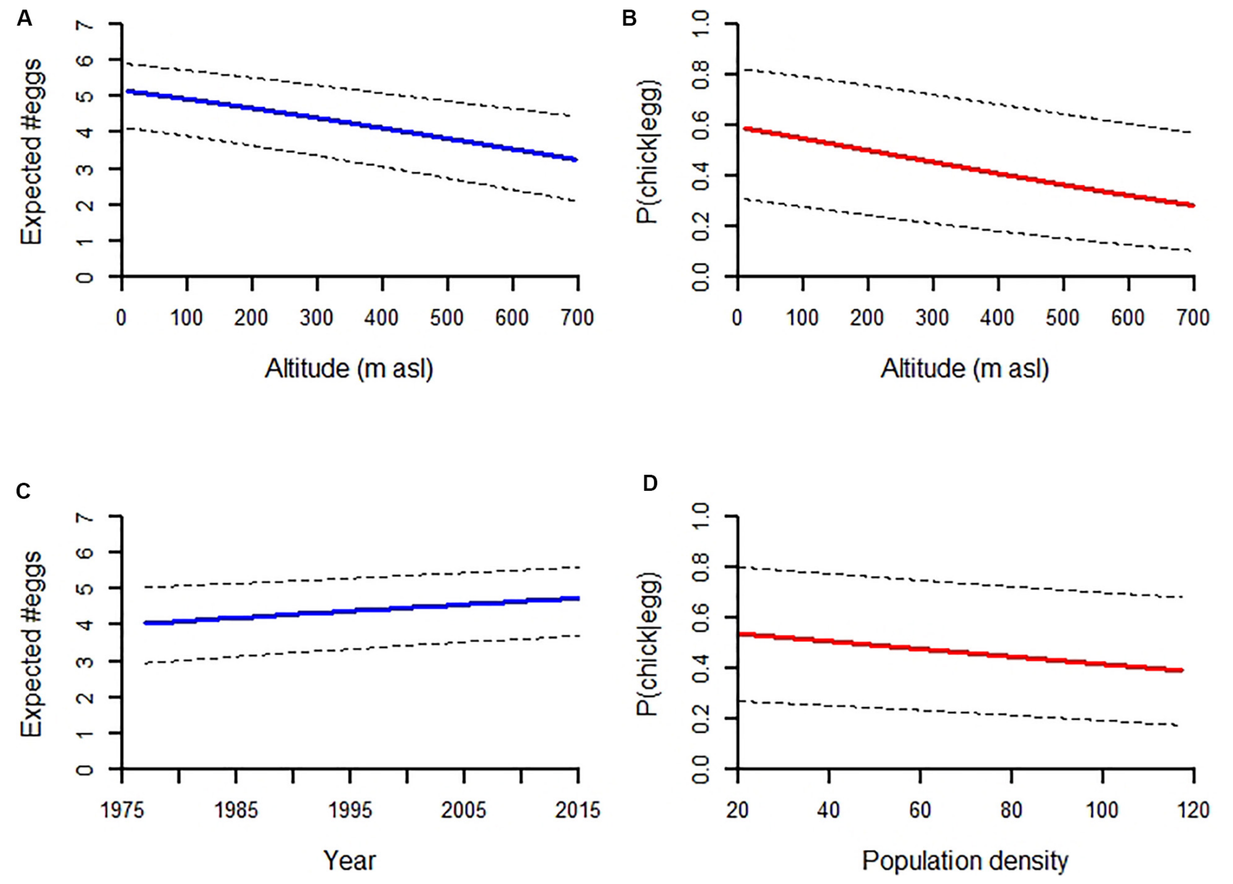

FIGURE 2 | The causes of variation in breeding success in the white-throated dipper population in River Lyngdalselva 1978–2015. Effects are based on model predictions: Influence of altitude on the **(A)** clutch and **(B)** brood size, the **(C)** temporal increase in clutch size, and the **(D)** density effect on brood size. *N* = 2585.

Sequential Monogamy

Before correcting for causality in the breeding success analysis, sequential monogamy was a major contributor to the model. Note, however, that our indicator for sequential monogamy indicated whether the female at any point in the season changed partner, and would thus be set before the change of partner actually took place. Females that later changed partner (during the same breeding season) usually failed at their first breeding attempt. There would therefore be a clear circularity in the analyses, overemphasizing the first failed breeding attempt of sequentially monogamous females, which could then trigger new breeding attempts and thus make partner change possible. This serves as an example demonstrating how potential errors in the analyses might arise due to faulty causality.

Yet, the rarity of sequential monogamy among females warrants further investigation. The first statistically strong but wrong result originated from curiously few field observations, where 40 breeding events (1.8%) by 38 females (3.2%) had a seemingly overwhelming effect when compared to the other 2125. We found no indication of over-dispersion in the number of sequentially monogamous breeding events for all females. Thus, we found no support for the notion that some females had an enhanced probability of sequential monogamy. We found mean temperature for the previous summer and autumn to be reliable explanatory variables for sequential monogamy. This climatic driver suggested that if the previous year was cold, there would be an increased probability of sequential monogamy the following breeding season.

Over-Dispersion

Over-dispersion suggested extra sources of variation not caught in the explanatory variables, i.e., that there were extra effects and phenomena not accounted for in the model. It was estimated to be negligible for clutch size. However, the over-dispersion for brood size given clutch size was estimated to be substantial ($\kappa = 0.59$, see **Supplementary Material 2**). When examining a model where the distributional modeling of over-dispersion was replaced with a per-measurement random factor, this factor stood for 88% of the overall variance contribution for number of chicks given the number of eggs. However, a look at the distribution of number of chicks for different number of eggs (see **Supplementary Figure S2.1** in the **Supplementary Material 2**), suggested that zero-inflation may have been the reason for the over-dispersion, further suggesting that failure at the batch-level as well as individual level may have reduced the hatching success.

DISCUSSION

Overall, territory location had a strong effect on the breeding success of the dippers, although local climatic variation also contributed. Birds breeding at higher altitudes further from the coast laid fewer eggs and fledged fewer young than dippers at lower altitudes closer to the coast. The altitudinal and coastal-inland gradients were most likely reflecting microclimatic variation; the microclimate would thus become progressively cooler while moving up the altitudinal gradient, by −0.65° per 100 m increase in altitude, and moving away from the coast to breeding locations further inland. The main river spread into smaller tributaries upstream, and reduced breeding success at higher altitudes could be a result of a generally lower food availability in smaller tributaries and perhaps reduced environmental buffering against flooding and drought events (Chiu et al., 2008). Reduced breeding success at higher altitudes could potentially also be a consequence of delayed breeding, because later breeding phenology is associated with lower fitness (Gamelon et al., 2018; Nilsson et al., 2019), although dippers are generally thought to breed multiple times during one breeding season (Fransson and Hall-Karlsson, 2008).

Earlier breeding might be the most commonly reported response to climate warming (Parmesan and Yohe, 2003; Dunn and Winkler, 2010), the dipper being no exception (Gamelon et al., 2018; Nilsson et al., 2019). In general, birds breeding earlier also produce larger clutches and more fledglings, although breeding time was not a significant contributor in this study. Accompanying earlier breeding in the dipper, the number of eggs in the clutch has increased during the study period. The increased clutch size might be a consequence of climate warming resulting in territories also at higher altitudes becoming available earlier, and increasing food availability prior to the breeding season in early spring. This would improve female body condition and enable females to lay more eggs. Thus, here we report a case of climate warming resulting in increased breeding effort, in addition to previous reports of earlier breeding (Parmesan and Yohe, 2003; Dunn and Winkler, 2010; Gamelon et al., 2018; Nilsson et al., 2019). Despite more eggs laid, there has not been a subsequent increase in the number of chicks fledged in the river system. The probability of fledging has not increased, probably because climate change has not only led to increased mean temperatures but also greater variability in the weather conditions (Easterling et al., 2000). Thus, greater climatic variation might reduce the dippers ability to forage efficiently enough to raise all chicks from hatching to fledging, due to droughts or sudden flooding events. An additional complicating factor is that the dippers in Lyngdalselva are partial migrants with the additional time constraint of arriving back on the breeding grounds ahead of breeding; the responses of partial migrants to climate change have proven difficult to predict (Berthold, 2001; Nilsson et al., 2006).

Location, or territory identity, had a substantial influence on the size of the brood, where some territories were consistently associated with a large number of nestlings, while others generally produced fewer nestlings. Specifically, location is a variable quantifying unknown and unmeasured but obviously important characteristics of the territory that might include habitat quality, local food abundance, nest site suitability, etc. Habitat quality obviously influences fitness (Newton, 1998), for example, in black kites *Milvus migrans*, high occupancy territories had higher food abundance and low predation risk, and produced most of the recruits (Sergio and Newton, 2003). Occupancy differed strongly between territories also in the present population (Nilsson et al., 2019).

We found that high population density had a negative effect on clutch size. Presumably, when population density was high, more of the low-quality territories were occupied, reducing the population average reproductive output. This is called density-dependent fecundity, the habitat heterogeneity hypothesis or the buffer effect, and explains how variation in breeding territory quality contributes to population dynamics (Brown, 1969; Dhondt et al., 1992; Mcpeek et al., 2001). Despite high population density favoring earlier breeding due to the competitive advantage of young fledging early (Nilsson et al., 2019), contradictorily high population density was associated with smaller clutches. Note that there were no density effects on brood size. From a population dynamical context, the contribution by strong fluctuations in winter mortality seemed to be greater than the relatively constant contribution by reproduction. In a long-term perspective, although successively warmer winters favor positive population growth, density-dependence can cause populations to become less buffered against occasional weather extremes (Gamelon et al., 2017).

Female and male age had an effect on clutch size, where the female effect was considerably stronger. Older females laid larger clutches than younger females. The female age effect on clutch size was not quadratic, contrary to earlier findings demonstrating a clear peak for female age in breeding phenology (Nilsson et al., 2019). Usually, age-specific reproductive output improves with age until leveling off (Forslund and Pärt, 1995). Presumably, reproduction improves with age and experience, while individuals with poor breeding performance might also suffer lower survival, which might contribute to explain the observed pattern (selective disappearance; Reid et al., 2003; McCleery et al., 2008). Thus, we did not find any evidence of senescence in female reproductive parameters (Monaghan et al., 2008). This might lend some support to the terminal investment hypothesis (Clutton-Brock, 1984; Duffield et al., 2017), which states that when an individual's chance of future reproduction grows smaller, the investment in current reproduction should increase. Although the effect of male age on clutch size was marginal, older males were associated with smaller clutches than younger males. This is in contrast to results from other study systems, where male age had no effect on clutch size (Sanz, 2002; Reid et al., 2003) or a positive effect (Mills, 1973; Hasselquist, 1998). However, Kindsvater and Alonzo (2014) found that when mortality is low, young females might reduce current clutch size and prioritize the next breeding opportunity. Male polygyny status had a negative effect on brood size where secondary females produced fewer young, possibly because polygynous males did not provide as much parental care as monogamous males (Slagsvold and Lifjeld, 1994).

Surprisingly, the climatic influence was of lesser consequence compared to other effects in explaining variation in clutch and brood sizes. Considering the importance of winter weather for population dynamics in this species (Nilsson et al., 2011a; Gamelon et al., 2017), the minor influence of weather in the following months is remarkable. Temperature regimes around the trigger date, meaning when the minimum temperatures had exceeded 0°C for five consecutive days, from 5 days before and until 9 days after, were most prominent. High maximum temperatures had a diminishing effect on clutch size while high minimum temperatures increased brood size. High minimum temperatures most likely improves feeding success and chick survival, because then there will most likely be less risk of temporary setbacks with freezing over of the river rendering prey inaccessible. In birds, spring temperature is a key determinant of timing of breeding (Parmesan and Yohe, 2003; Charmantier et al., 2008; Nilsson et al., 2019), and the negative effect of high maximum temperatures on clutch size might indicate that birds have failed to time-optimize laying date, leading to a reduced clutch. Interestingly, high maximum temperatures the previous autumn enabled dippers to raise more chicks. Presumably, this is an effect of improved adult body condition in early winter, enabling dippers to invest more energy into parental care, despite similar clutch sizes. Higher winter river discharge in a 2-week period 1 month before the trigger date had a positive effect on both clutch and brood size. Given that one of the discharge variables were a threshold variable for when discharge dropped below 10 l/s at each nest site, we conclude that higher river discharge in late winter naturally is positive for dipper reproductive success. Water birds are well known to be affected by floods and droughts (Royan et al., 2013), and dipper prey might become more inaccessible during flooding events (Chiu et al., 2008, 2013), because dippers are visual predators and floods lead to high water turbidity. Droughts during breeding might reduce the available river area used for foraging, but more importantly, it may render the nest visible to predators because dipper nest sites are selected for their ability to flush away chick excrements (Tyler and Ormerod, 1994). Because dippers depend entirely on submerged prey and rapidly running water to hide the nest, the absence of discharge variables of high importance for breeding success is rather unexpected. Presumably, the dipper has adapted to the natural variation in river discharge by choosing nest sites where droughts rarely occur and foraging at alternative sites with shallow water, such as swells and lakes, during floods.

Important Reflections From Analyzing Sequential Monogamy

Investigating sequential monogamy, the only variable able to explain some of the variation was the mean temperature during the previous summer and autumn. The probability of sequential monogamy increased with decreasing temperatures, indicating that sequential monogamy might be related to poor body condition. Body condition during molt and establishment of wintering territories in late summer and autumn, prior to the critical winter months, might carry over to the breeding season (Harrison et al., 2011), where females in poor condition make the best of a bad situation. Neither did we find support for the notion that some females have an enhanced probability of sequential monogamous breeding events; two females showed this behavior twice, which is not implying that these females had a penchant for sequential monogamy. Worth noting, the observed number of sequentially monogamous breeding attempts is a conservative measure, because to detect sequentially monogamous breeding events a large field effort is required during the early breeding season, and some events might have passed under the radar. Incidentally, extra-pair paternity seems to be low in the dipper, approximately 2% (Øigarden and Linløkken, 2010), but it would be interesting to know whether the frequency is higher in sequentially monogamous females. For a discussion about circularity in statistical analyses of biological systems, see the **Supplementary Material 2**.

Conclusion

Low occupancy, and presumably low quality, territories in years of high population density lead to reduced fledging success, also called density-dependent fecundity (Brown, 1969; Dhondt et al., 1992; Mcpeek et al., 2001). Breeding success in the dipper was heavily dependent on the territory the breeding pair defended; there is therefore fierce competition for the best territories in the river system. The differential rates of occupancy between the territories in the population has thus received its natural explanation (Nilsson et al., 2019). In addition to the territory effect, females laid larger clutches at the end of the study period than at the start of it. Considering the climate warming in the study area, female body condition might have improved due to milder pre-breeding weather, and territories at higher altitudes might have become available earlier than at the start of the study. Increased clutch size is thus presumably explained by climatic factors, and it is for that reason surprising that climatic conditions explained comparatively little of the variation in fledging success. Hitherto, dipper breeding success might have been buffered against negative effects of climate change. Whether this can continue under further warming trends and increasing incidences of weather extremes is presently unknown, but long-term studies remain important in predicting future climate responses (Gamelon et al., 2017).

DATA AVAILABILITY STATEMENT

The code used in this analysis is available at https://github.com/trondreitan/egg_chick_intervals. The datasets analyzed during the current study are not publicly available, due to it being a private, unique long-term collection of individual data on a breeding dipper population, which has cost an enormous effort in the field 1973–present. However, the data are available from the corresponding author upon reasonable request. The complete dipper data are stored at the Norwegian University of Life Sciences, and managed by OWR (ole.rostad@nmbu.no).

ETHICS STATEMENT

The field work was conducted with respect for the animals' well-being and adheres to the Guidelines for the Use of Animals in Research (Anonymous, 2006). It complies with the laws and regulations for animals used in research in Norway (FOR-2003-03-18-349, LOV-2009-06-19-100, LOV-1981-05-29-38§26). Ethical approval is not required for bird ringing (FOR-2003-03-18-349§§21-24), but Ringing licenses were issued and approved by the Norwegian Bird Ringing Centre on behalf of the Norwegian Environment Agency.

AUTHOR CONTRIBUTIONS

ALKN and JHLL conceived the study. KJ collected the field data. TSk ran the hydrological simulations and also provided DDD model input for the analyses. OWR organized the dipper data collection. TR conducted the analyses. ALKN and TR wrote the paper with input from MG, TSl, LAV, TSk, OWR, BW, KJ, and NCS. All authors contributed to the article and approved of the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.542846/full#supplementary-material

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Elevational Gradients as a Model for Understanding Associations Among Temperature, Breeding Phenology and Success

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Climate change is associated with advancing phenology of seasonal traits in many taxa, but shifts by higher trophic levels are generally reduced compared with those of lower trophic levels. For example, the eclosion date of caterpillars and the lay date of insectivorous passerine birds have both advanced recently, but the former has done so more than the latter. While the ensuring phenological mismatch between predator and prey is well-documented, our understanding of the origins of this mismatch is more limited. Here we shed light on the interplay between ambient temperature, breeding phenology and reproductive success in a single population of blue tits (*Cyanistes caeruleus*) nesting over a 1,000 m (∼5°C) elevational gradient in the French Pyrenees. During the 6 years of this study, we found that average breeding phenology varied by 2–9 days among years, but was on average 11 days earlier at low versus high elevation. Despite the delay, breeding at high elevation was associated with lower and more variable temperatures during breeding. Early breeders within a given year generally had larger clutch sizes than late breeders, which led to more offspring fledged as typically found in other studies. However, in three of the 6 years, the probability of producing fledglings was actually lower among early layers. Additionally, birds breeding at high elevations who experience conditions typical of early breeders in other populations had reduced hatching success and were significantly less likely to fledge any young compared with those breeding at lower elevation. Reduced success at high elevation was not obviously driven by higher nest predation, which was exceptionally low, or reduced food availability because high elevation birds laid clutches of comparable size and fledged the same number of offspring of comparable mass as those breeding at low elevation. Our study reveals the capacity for substantial variation in breeding phenology within a population, but that the success of early breeders varies across years and temperature gradients. We suggest that the evolution of phenological advancements by small endotherms might be curtailed by increased probability of experiencing, and failure under, challenging meteorological conditions in late winter or very early spring.

Keywords: *Cyanistes caeruleus*, environmental cline, environmental constraints, phenotypic plasticity, reproductive investment

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INTRODUCTION

Recent meta-analyses show that organisms of diverse taxonomic groups are responding to earlier springs by advancing the timing of key life events (Thackeray et al., 2010, 2016). However, there appears to be variation in the extent of advances across trophic levels, with lower trophic levels advancing their phenology more than higher levels (Both et al., 2009b; Thackeray et al., 2010). A classic example is seen in invertebrates and insectivorous birds breeding in northern temperate latitudes, with invertebrate prey advancing their date of emergence more than predatory birds are advancing their lay dates (Visser et al., 1998; Both et al., 2009a,b). This differential in phenological change leads to the well-documented concept of phenological mismatch, with predators increasingly rearing their offspring after the peak of prey availability (e.g., Durant et al., 2007; Visser et al., 2012). However, why this mismatch should arise is not clear. One possibility is that, with their faster generation times, prey are able to evolve adaptive responses to advancing springs more rapidly than predators with longer generation times (Cushing, 1969; Visser and Both, 2005). Another possibility, however, is that endothermic predators, such as birds, are constrained from advancing breeding phenology to the same extent as their invertebrate prey because they suffer more directly and/or indirectly from cold weather (Visser et al., 2015). While climate is warming and springs are advancing, weather can be prohibitively cold early in the year because day lengths are shorter, resulting in weakened selection for ever-advancing breeding phenology in endothermic predators. Testing this 'environmental constraints' hypothesis requires investigating the interplay between temperature, breeding phenology and success which can be challenging in natural settings.

For example, the obvious way of exploring this interplay is to investigate the relationship between breeding phenology and success throughout a breeding season, but such an approach is not valid. This is because although early breeding should be associated with colder weather, it will typically be associated with a closer match to peak prey availability (Verhulst and Tinbergen, 1991; Winkler and Allen, 1996; Verhulst and Nilsson, 2008; Emmenegger et al., 2014), which will confound the expected positive relationship between temperature and breeding success under the environmental constraints hypothesis. Indeed, early breeding is typically associated with increased, not reduced, success (Kluyver, 1951; Verhulst and Tinbergen, 1991; Barba et al., 1995; McCleery and Perrins, 1998). An alternative approach is to compare the relationship between phenology and success among years that vary in average temperature, although the magnitude of any effect measured is contingent upon the magnitude of inter-annual variation in temperature, which is often modest. Nevertheless, long-term longitudinal studies capturing sufficient inter-annual temperature variation provide some evidence for the environmental constraints hypothesis. For example, a 24-yearlong study in pied flycatchers (*Ficedula hypoleuca*) showed that low temperatures during early breeding are associated with reductions in fledging success (Moreno et al., 2015). Similarly, in blue tits (*Cyanistes caeruleus*) low temperatures during egg-laying was linked to hatching delays and reduced breeding success (Kluen et al., 2011). Whilst such longitudinal studies clearly provide important insights into the associations among ambient temperature, breeding phenology and success, their duration also means that the results are likely to be driven by a combination of plasticity and adaptation (Charmantier et al., 2008; Ramakers et al., 2019). Further, the inevitable time taken to establish such studies coupled with the pressing need to understand such relationships in a time of rapid climate change, provides an incentive for alternative approaches.

One complementary approach might be to use elevational gradients within a single population of a given species as a means of investigating temperature effects on breeding phenology and its impacts on metrics of breeding success. Such an approach can work in principal because temperature declines linearly with elevation: ~0.65°C for every increase in elevation of 100 m, but day length stays constant across the gradient. In accordance, recent meta-analytical (Boyle et al., 2016) and survey-based (Saracco et al., 2019) approaches demonstrate that avian breeding phenology is delayed at higher elevations. However, a potential problem is that habitat structure and invertebrate prey abundance might also vary across extensive elevational gradients and do so non-linearly (Körner, 2007; Nice et al., 2019) confounding the ability to surrogate temperature through elevation. To reduce the impact of these potential confounds we need a targeted elevational approach that provides representative variation in temperatures expected under climate change, but minimizes systematic variation in other significant ecological parameters, principally habitat type, cover from predators and food types or abundance. However, few previous studies have used such a targeted elevational approach, meaning effects might often be influenced by significant habitat differences, day length or local adaptation (Boyle et al., 2016).

Here we used a targeted elevation approach in the French Pyrenees to investigate the associations among elevation, breeding phenology and success in a nest box population of blue tits (*C. caeruleus*) across 6 years. Our approach is targeted in two ways. First, the ~600 nest boxes are located within 5 main areas of contiguous habitat and were within 16 km of each other (median = 5 km). This distance is well within the known dispersal distance of blue tits (Paradis et al., 1998) and indeed we have observed several instances of among-site dispersal. Thus, our nest boxes encapsulate a single breeding population of blue tits. Second, the elevational gradient is a relatively modest 1,000 m and critically stops at 1,530 m a.s.l, ~300 m below the upper end of the deciduous tree line in the French Pyrenees. While this range is sufficient to generate a ~5°C difference in mean daily (24 h) between low and high elevations, it is insufficient to have a major impact on habitat. For example, the habitat is characterized by mixed deciduous woodland across the elevation gradient with no obvious differences in tree height, and all species are represented at all elevations, although there is a shift from oak (*Quercus robur*) domination to beech (*Fagus sylvatica*) domination with increasing elevation (Bründl, 2018). Finally, observations of nestling provisioning show that feeding rates marginally decrease but that prey type delivered is comparable across the elevational gradient (Bründl, 2018). Thus, our available evidence suggests that our elevation gradient can be used as a natural experiment to investigate the influence of temperature variation on breeding phenology and success, without significant confounds of local adaptation or ecology.

The blue tit is a short-lived, small passerine bird with high fecundity (Perrins, 1979). Previous longitudinal studies have shown that they adjust lay date in response to spring temperatures and that clutch size and fledging success generally decline with delayed phenology (e.g., Haywood, 1993; Lambrechts et al., 1996; Källander et al., 2017; Shutt et al., 2019). However, cold temperatures during egg-laying have been shown to reduce the success of early breeders through reduced hatching success and lower nestling body mass in a Finnish population of blue tits, providing some evidence of the environmental constraints hypothesis (Kluen et al., 2011). First, we describe elevational (1,000 m) and annual (2012–2017) variation in breeding phenology, and its effects on average temperatures experienced during incubation and nestling provisioning. Second, we investigate the associations among year, elevation and lay date, on clutch size and hatching success. Finally, we test the effects of each on fledging success and nestling mass. The environmental constraints hypothesis predicts that advanced breeding phenology is associated with reduced temperatures during breeding, and that as a consequence metrics of breeding success will be reduced among early breeders in some years particularly at high elevations.

MATERIALS AND METHODS

Study Population and Habitat

Climate and reproductive data were collected near the research Station for Theoretical and Experimental Ecology of Moulis (SETE, UMR 5321; 42°57′29′′ N, 1°05′12′′ E), in the French Pyrenees during the breeding seasons 2012–2017. Overall, our 14 woodlots within 5 main sites contained a total of 626–641 Woodcrete Schwegler^{TM} 2 M nest boxes (32 mm entrance hole diameter) per year spaced at ∼50 m intervals from 430 to 1,530 m elevation (**Figure 1**). The median pair-wise distance between woodlots was 5 km (range = 0.6–16 km). All woodlots are connected by a contiguous mosaic of mixed deciduous woodland, primarily oak (*Quercus robur*), ash (*Fraxinus excelsior*), hazel (*Corylus avellana*), and beech (*Fagus sylvatica*), with the former three species being more common at lower elevations and beech at higher elevations. Temperature data was recorded from the 2015 breeding season at three locations across the elevational gradient (565, 847, and 1,335 m a.s.l.) using Tinytag^{TM} loggers (TGP-4500 and TGP-4505) positioned on tree trunks 2 m from the ground. This temperature data, which was recorded every 30 min, allows us to clarify temperature differences during incubation and nestling as a function of lay date across the elevational gradient. We, therefore, use the temperature data to validate the utility of using elevation gradients as a means of examining potential associations between temperature and breeding parameters. But we did not analyze detailed impacts of temperature *per se* as it is limited to just three sites in three years and is highly correlated with elevation. Precipitation was not included as it is not expected to decrease in a linear fashion with elevation (see Körner, 2007). Overall, temperature decreased by an average 5°C along the elevational cline throughout the breeding season (see section "Results" for specific details).

Breeding Phenology, Investment and Success

We recorded lay date, clutch size, hatching failure and fledging success in all years (2012–2017). Each of these parameters was known with precision owing to nest checks every 3–5 days, which increased to daily during critical periods. These critical periods were before the onset of laying for recording lay date, from the sixth egg to clutch completion to determine clutch size and the start of incubation, from day 11 of incubation to determine hatching and from day 18 after nestling hatching to determine fledging success. Our blue tit population is single brooded, although pairs are known to make a second nesting attempt if the initial brood is abandoned early in the season (personal observations). No differentiation between first and any second attempts was possible, since blue tits are known to also use natural cavities in our population. Nevertheless, abandonment is uncommon overall (10% of 535 nesting attempts) and is uninfluenced by elevation (**Supplementary Figure 1**). In this study, we removed the 16 nesting attempts that abandoned before the onset of egg-laying from all analyses, and removed the 41 that abandoned during incubation from analyses of hatching and post-hatching analyses. As these latter cases were late in the season, they presumably occurred in response to declining food supplies. Thus the total number of hatchlings was determined as the number of eggs that hatched successfully from clutches wherein at least one hatched. The total number of fledglings was estimated as the number of nestlings at ringing (ca. day 15) minus those found dead after the rest of the brood fledged. Starting in 2013, all nestlings were weighed to the nearest 0.1 g (days 11–18 after hatching) using electronic scales. Our full data set comprised 519 blue tit nests for which lay date was known with precision and a full clutch of eggs was laid. However, this sample was reduced in subsequent analyses owing to rare cases of missing observations, the use of some nests in experiments for other purposes and nest abandonment. In 2013–2014, 58 experimental nests were excluded from the clutch size analysis, as we modified egg-laying in these nests ($N = 461$ remaining). However, this manipulation did not affect subsequent breeding parameters, since variation in the number of eggs incubated and hatchling numbers were returned to natural levels at incubation onset (Bründl et al., 2019). The precise sample size for each analysis is provided below.

Statistical Analyses

Statistical analyses were performed in the *R* environment, version 3.5.1 (R Core Team, 2018). Distributions of dependent variables and model residuals were visually inspected for normality. Normal response terms were analyzed using linear models (LMs) in the standard 'stats' package (R Core Team, 2018). If the data were non-normal, generalized linear models (GLMs, package = MASS; Venables and Ripley, 2002) were used adjusting residual variance structure accordingly, i.e., the error distribution family and link function (see SOM tables of each analysis;

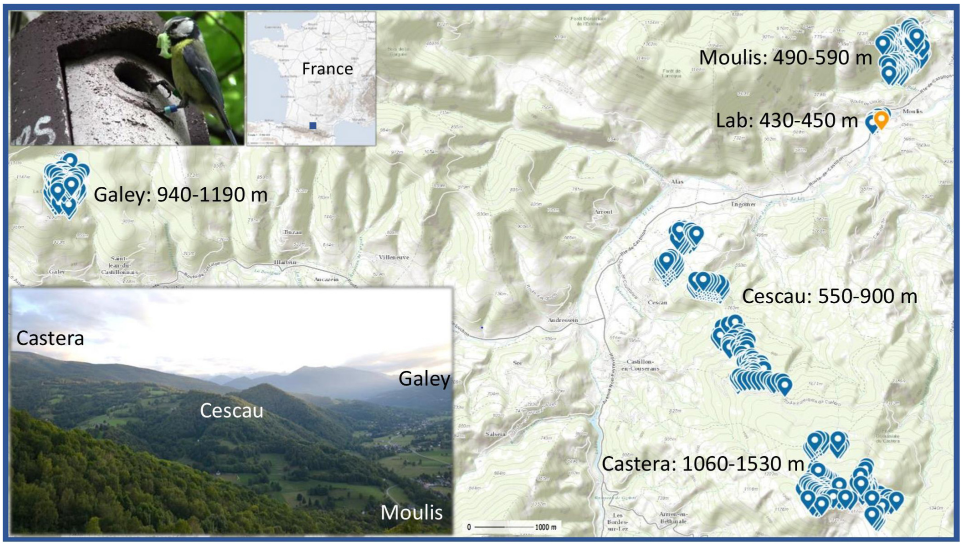

FIGURE 1 | Topographic map of the study site near the research Station for Theoretical and Experimental Ecology of Moulis (42°57′29′′ N, 1°05′12′′ E, orange marker), in the French Pyrenees. A total of 626–641 nest boxes (blue markers) are spaced at ca. 50 m intervals across 14 woodlots, divided into 5 sites, from 430–1,530 m elevation. The site names with their elevational ranges are provided. The woodlots are situated within a contiguous mosaic of mixed deciduous woodland (see bottom photo). Scale = 1:42000. The top map shows the sites' location within France. Map generated by l'Institut National de l'Information Géographique et Forestiére (© IGN, 2020) via 'Geoportail.gouv.fr'. The top photo shows a banded blue tit delivering a caterpillar to its nest box.

Thomas et al., 2013). Fitting nest box identity as random terms in the models explained none of the variance and had no qualitative impact on the results (see **Supplementary Table 1**), presumably because the number of nest boxes far exceeded those occupied by blue tits and the inter-annual survival and philopatry of breeders were low [21% for banded females returned to breed in a nest box in a subsequent year (mean number of breeding attempts = 1.2 per banded female, maximum = 4)]. To test the effect of the random term we used corrected Akaike's Information Criterion (AICc – for finite sample sizes) set to a Delta of two (Zuur et al., 2009). Nest box identity was thus removed as a random term from all the subsequent, non-mixed models. All models underwent checks for overdispersion and heteroscedasticity of residuals (Zuur et al., 2009). Collinearity among explanatory terms was tested using a variance inflation factor (VIF) analysis (package = car; Fox et al., 2018) which if above 3–7 degrees indicates biased high contribution of a variable to the standard error of a regression, i.e., multicollinearity (Zuur et al., 2010; Dormann et al., 2013). However, the VIF between the main potential collinear terms of lay date and elevation was low (1.22) and thus both were included as continuous variables in the same models. Non-mixed model selection was based on changes in deviance between full models and models excluding each factor using the ANOVA function in *R* (significance set at $\alpha < 0.05$) (Zuur et al., 2009).

Overall, we conducted six basic models pertaining to: breeding phenology (lay date); clutch size; hatching success; the probability that at least one nestling fledged; the number of nestlings fledged from successful nests and mean nestling mass per brood. In all models, we fitted lay date (except in the lay date analysis), elevation, and year as the primary fixed terms of interest, as well as two-way interactions including lay date and/or elevation, year and clutch size (see S2–S7 for more details). Although elevation was fitted as a linear predictor in all statistical models, we sometimes split the elevational gradient into three elevational ranges in figures to facilitate visualization and interpretation only (see Figures). The three categories – low (430–633 m), mid (702–904 m), and high (923–1,530 m) elevations – were determined where the greatest gaps in elevation between occupied nest boxes were observed (see also Schöll et al., 2016), and corresponded to the location of the temperature data loggers (central in each elevational range). We included the possibility of a non-linear (2nd order polynomial) main effect of lay date since the success of very early and late nests might be expected to be compromised, but it was never significant (**Supplementary Tables 3–7**). However, elevation was included only as a linear term as we have no clear predictions about non-linear effects and visualization of raw data suggested that no non-linear patterns between elevation and y parameters were likely to be present.

First, we investigated how breeding phenology (lay date) varied with elevation and year ($N = 519$). Second, we analyzed how clutch size was affected by lay date, elevation and year ($N = 461$), including both the separate effects of elevation and lay date on clutch size and the interaction between the two variables. LMs with normal error structure were applied for both lay date and clutch size analyses. To investigate the probability of hatch failure, i.e., whether or not nests failed to hatch any eggs, we applied a GLM with binomial error structure ($N = 476$). In this model, the number of eggs incubated was fitted as a covariate since the area of large clutches exceeds the area of the brood patch, making them more challenging to incubate (Haftorn, 1983; Engstrand and Bryant, 2002; Niizuma et al., 2005). Fledging success was investigated as a two-step process: first by investigating the factors associated with the probability of fledging at least one nestling (excluding nests with no hatchlings; $N = 438$), and second, for those that did fledge at least one offspring, the factors influencing the number of nestlings that fledged ($N = 369$; 16% of the 438 nests failed to fledge young). This two-step process was performed because alternative zero-inflated methods failed to converge when the interactions central to the question were included. Finally, we also investigated factors affecting mean nestling mass per brood in a LM ($N = 345$ broods with 2,230 nestlings). In addition to the primary predictors of interest (lay date, elevation and year), linear and quadratic effects of brood age and brood size were added as covariates. We fitted brood age rather than linear predictors, such as tarsus, since age was known with precision, and tarsus length is itself a partly condition-dependent trait (Merilä and Fry, 1998).

RESULTS

Elevation and Year Effects on Phenology and Consequences for Temperatures During Incubation and Nestling Provisioning

Over the 6 years of study, clutches were initiated between 27 March and 11 June, with a mean of 16 April [±10 days (SD), $N = 519$ total breeding attempts; **Table 1**]. Some late nesting attempts are likely to be explained by re-clutching following rare early abandonment or failure, but blue tits are not double-brooded in our population. Both elevation and year had a significant impact on average breeding phenology (elevation: $F_{1,512} = 184.96$, $P < 0.001$; year: $F_{5,512} = 32.31$, $P < 0.001$; **Supplementary Table 2**). More specifically, the mean lay date was 13 April at low elevations (430–633 m) (±7 SD), but averaged 5 days later at mid elevations (702–904 m) (18 April ±12 SD), and 11 days later at high elevations (923–1,438 m) (24 April ±15 SD) (**Figure 2A**). Similarly, for example, lay dates were an average of 7 days earlier in 2017 and 5 days later in 2013 than the overall mean of the population across all years (**Table 1**). Finally, there was a significant interaction between year and elevation on lay dates, with lay date being delayed to a greater extent at high elevation in some years (e.g., 2013) than others (e.g., 2017) ($F_{5,507} = 8.46$, $P < 0.001$; **Figure 2B**).

Early and high elevation breeding were associated with reduced and more variable temperatures during incubation and nestling provisioning. For example, at low elevation, early breeders, as opposed to late breeders, experienced average day-time temperatures (7 am – 7 pm) that were ∼2°C lower during both incubation (∼12 vs. ∼14°C; **Figure 2C**) and nestling rearing (∼13 vs. ∼15°C; **Figure 2D**). At high elevation, early breeders experienced temperatures that were ∼4°C lower than late breeders during incubation (∼8 vs. ∼12°C), although temperatures during nestling rearing averaged ∼11°C irrespective of phenology. In addition, early phenology, particularly at high elevation, was associated with high coefficients of variation in temperatures during breeding. In this case, early breeding at low elevation was associated with twofold greater variation in day time temperatures during incubation and fourfold greater variation at high elevation (**Figure 2E**). During nestling rearing, early breeders experienced double the variation in day-time temperatures at low elevation and three times the variation at high elevation, compared with late breeders (**Figure 2F**). These results support the assumption of the environmental constraints hypothesis that early breeding is associated with lower and more variable temperatures. The question is, are temperatures early in the season and at high elevation sufficiently low (on average or through greater variability) to compromise metrics of success, as predicted by the environmental constraints hypothesis?

TABLE 1 | Breeding phenology across 6 years (2012–2017) at 3 elevational categories [low (430–633 m), mid (702–904 m), and high (923–1,530 m)] and per year.

Year	*N*	Mean	±*SD*	Min	Max
Low					
2012	43	13 April	8.3	04 April	17 May
2013	46	17 April	2.2	11 April	23 April
2014	54	11 April	7.9	27 March	12 May
2015	63	17 April	5.4	04 April	08 May
2016	65	13 April	6.8	27 March	05 May
2017	82	08 April	6.2	30 March	17 May
Mid					
2012	8	13 April	6.9	05 April	26 April
2013	10	29 April	19.1	17 April	07 June
2014	18	17 April	10.6	09 April	13 May
2015	14	19 April	2.3	16 April	22 April
2016	18	22 April	12.0	06 April	02 June
2017	24	10 April	7.4	01 April	09 May
High					
2012	5	30 April	5.5	23 April	08 May
2013	4	06 May	9.0	28 April	17 May
2014	19	25 April	18.7	12 April	11 June
2015	9	01 May	13.5	18 April	01 June
2016	12	02 May	11.8	20 April	29 May
2017	25	12 April	5.2	30 March	23 April
Overall	519	16 April	10.3	27 March	11 June

Elevational and Annual Variation in Clutch Size and Hatching Success

Average clutch size in our population was 8.2 eggs (±1.4 SD, range: 4–12; **Supplementary Table 3**). The greatest contributor to variation in clutch size was lay date, with clutch size declining by one egg for every 2-week delay in the onset of laying over the ∼2 months laying period ($F_{1,453} = 99.11$, $P < 0.001$; **Supplementary Table 3**). After controlling for effects of lay date, we found that clutch size increased with elevation ($F_{1,453} = 14.54$, $P < 0.001$; **Figure 3A**) and varied among years ($F_{5,453} = 4.41$, $P < 0.001$; **Figure 3B**). For a given lay date, clutches were on average 0.6 eggs (8%) larger at high elevation compared with low elevation and differed by up to 0.8 eggs (9%) between years (e.g., 2013 versus 2015). Elevation failed to predict clutch size in the

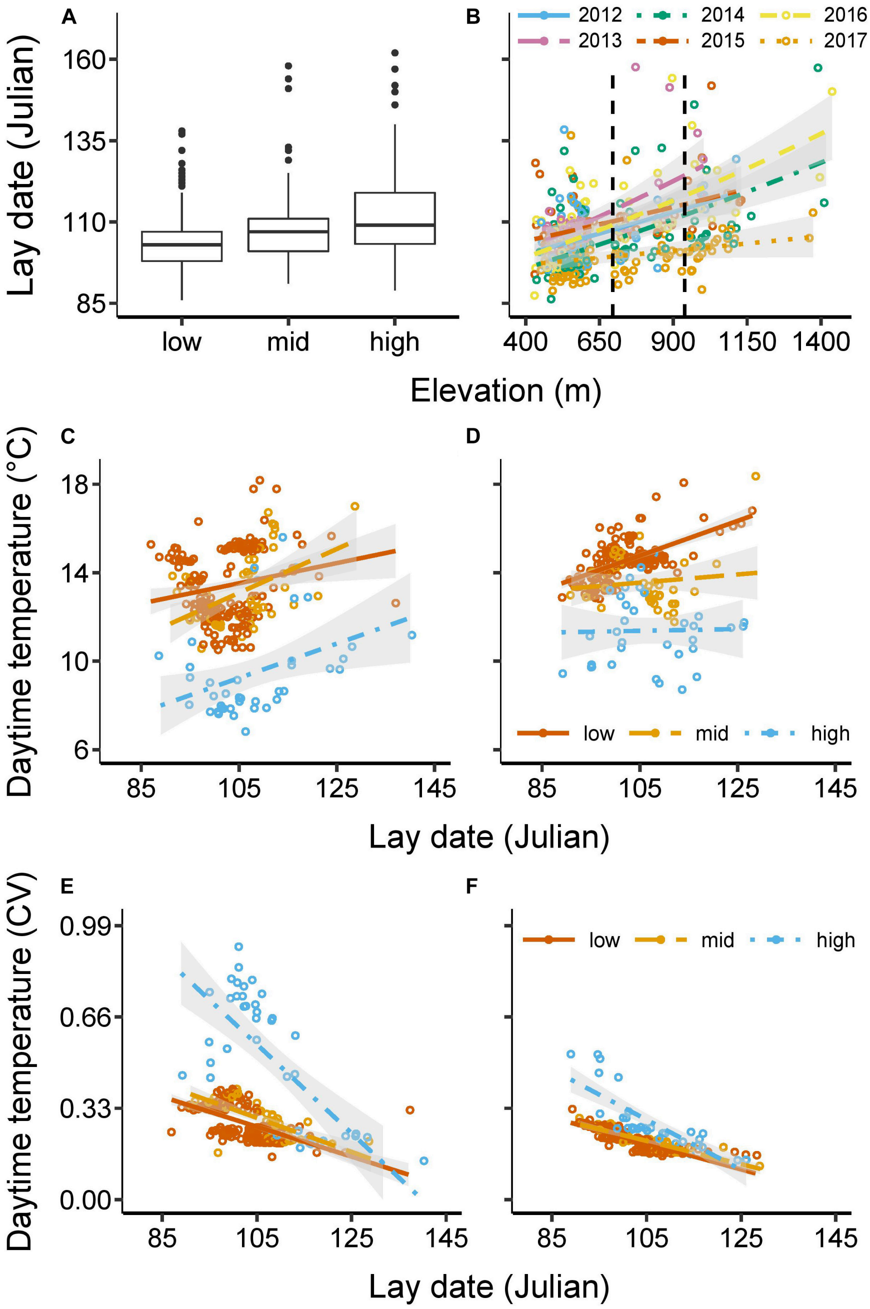

FIGURE 2 | Breeding phenology and temperatures. Figure **(A)** shows the median, interquartile range, minimum and maximum range, and outliers of lay date at 3 elevational categories [low (430–633 m), mid (702–904 m), high (923–1,438 m); *N* = 519, see also **Table 1**]. Figure **(B)** shows the interaction between elevation and year on lay date (e.g., lay dates were delayed at high elevations especially in 2013, while in 2017 the delay was more modest). (Vertical, dashed lines indicate the cut-offs for the elevational categories). Figures **(C–F)** show the average **(C)** and coefficient of variation **(D)** of daytime temperature experienced during the 10–20 days (mean = 14 days) of incubation for each nest (°C) as a function of lay date and elevational category (*N* = 287 nests); while **(E)** shows the average and **(F)** shows the coefficient of variation of daytime temperatures experienced during the 17–26 days (mean = 21 days) of nestling provisioning (°C) as a function of lay date and elevational category (*N* = 248 nests). Daytime temperatures **(C–F)** were measured every 30 min between 7 am and 7 pm in 2015–2017 at 565, 847, and 1,335 m. All dates are in Julian units: 100 = 10 April in non-leap years/ = 9 April in leap years. All data are based on raw values, with lines representing best fits with 95% confidence intervals.

absence of lay date in the model, and the trend was reversed (estimate: −0.00046, $F_{1,454}$ = 1.82, P = 0.18; **Supplementary Figure 2**). In other words, clutch sizes were only larger at higher elevations relative to their later lay dates, but in absolute terms were of comparable size to those at low elevation despite their later phenology. We found no evidence to suggest that clutch size

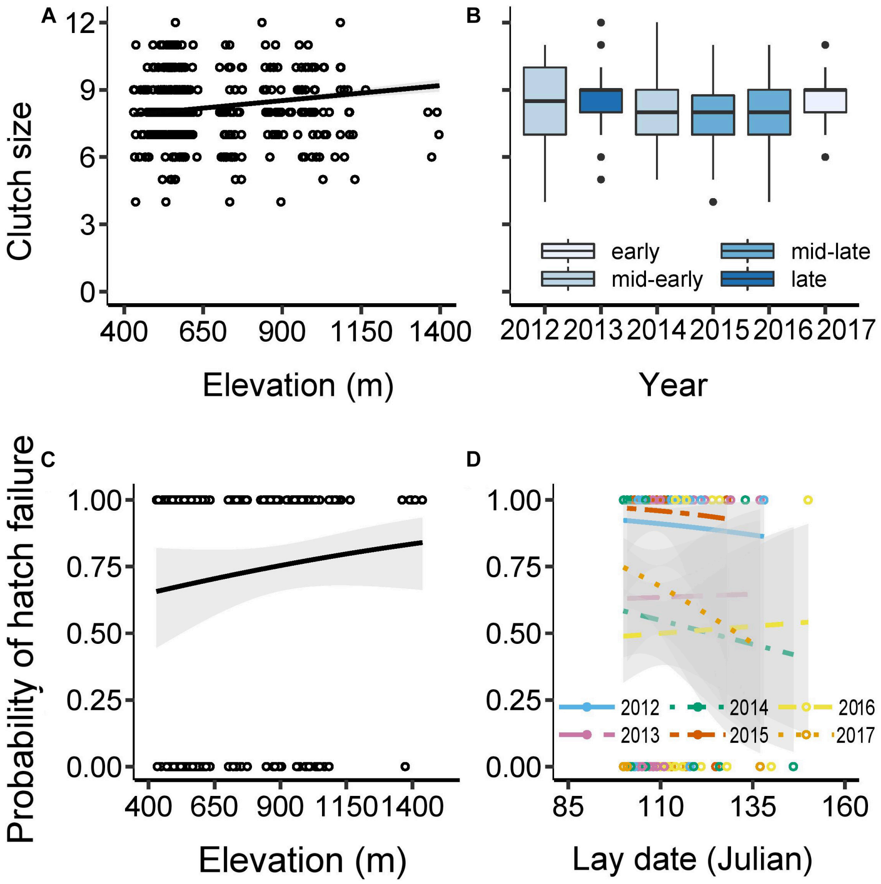

FIGURE 3 | Clutch size and hatching success. Clutch size as a function of: **(A)** elevation across the 6 years (figure shows raw data with predicted line controlling for effects of lay date and year); and **(B)** year (2012–2017) [boxplots generated from raw data and colored according to average lay dates for each year for illustrative purposes (see **Table 1**)]. Probability that at least 1 egg failed to hatch in a clutch as a function of: **(C)** elevation (m) [figure shows raw values and predicted line controlling for effects of the number of eggs incubated and year]; and **(D)** lay date [Julian: 100 = 10 April (9 in leap years)] and year (figure shows raw values and predicted line controlling for the effects of the number of eggs incubated and elevation). Clutch size analyses were based on GLM with normal error structures; *N* = 461 clutches; while hatching failure analyses were based on GLM with binomial error structure and logit link function; *N* = 476 clutches. The difference in sample size arose because 58 experimental nests were excluded from the clutch size analysis, as we modified egg-laying in these nests, though this did not affect hatching (see **Supplementary Tables 3, 4** for further details). 95% confidence intervals are presented around lines.

was influenced by interactions between lay date and elevation or lay date and year (**Supplementary Table 3**).

After excluding nests with complete hatch failure (see section "Materials and Methods"), we found that in 62% of nests at least one egg remained unhatched (mode = 0, range = 0-8 unhatched eggs), leading to an average of 6.9 hatchlings per nest (±1.8 SD, range: 1–11). Hatching success was not affected by lay date ($\chi^2_{1,465} = -0.41$, $P = 0.52$), but was influenced by clutch size, elevation and year (**Supplementary Table 4**). Larger clutches were more likely to be associated with at least one egg failing to hatch ($\chi^2_{1,466} = -8.16$, $P = 0.0043$). The probability of partial hatching success also increased with elevation ($\chi^2_{1,466} = -6.48$, $P = 0.011$), with an average of 7% more clutches failing to hatch all eggs at high versus low elevations (**Figure 3C**). The probability that all eggs hatched in clutches varied significantly among years, with almost all clutches in the mid-early year of 2012 and mid-late year of 2015 having at least one egg remaining unhatched, while significantly fewer nests (50–75% overall) had unhatched eggs in the other years ($\chi^2_{5,466} = -71.49$, $P < 0.001$, **Figure 3D**). An apparently significant interaction between lay date and year was found to be driven by two late nests in 2015, and no other two-way interactions involving lay date, elevation, year and number of eggs incubated were significant (**Figure 3D**, **Supplementary Figure 3**, and **Supplementary Table 4**).

Fledgling Production

The average percentage of nests fledging at least one nestling was 84% (excluding nests with no hatchlings; *N* = 438, **Supplementary Table 5**). The probability that at least one nestling fledged from such nests was negatively affected by elevation, declining by ~45% across the 1,000 m gradient ($\chi^2_{1,436} = -12.67$, $P < 0.001$) (**Figure 4A**). There was no statistically significant main effect of lay date ($\chi^2_{1,435} = -2.28$, $P = 0.13$) or year ($\chi^2_{5,430} = -7.78$, $P = 0.17$) on fledging success, although there was a significant interaction between the two

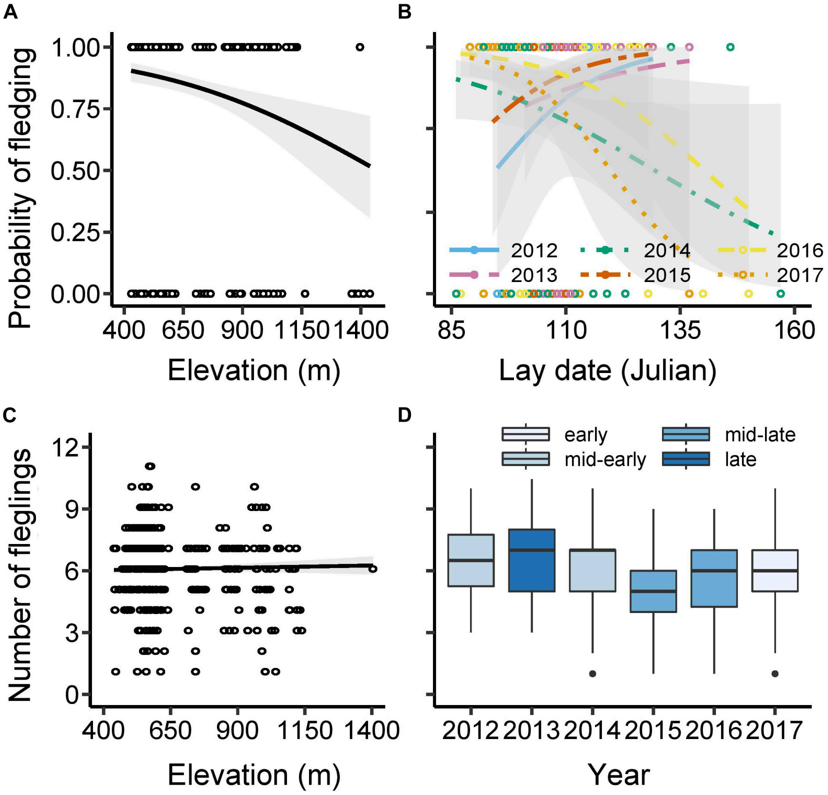

FIGURE 4 | Fledging success. The probability of at least 1 hatchling fledging the nest as a function of: **(A)** elevation (figure shows raw data with best-fit line); **(B)** lay date (Julian, see previous legends) and year (figure shows raw data and predicted lines controlling for the effect of elevation). The number of fledglings per successful nest (i.e., those with ≥1 fledgling) as a function of: **(C)** elevation (figure shows raw values with predicted line controlling for lay date and year); and [**(D)** year (box plots based on raw values showing median, interquartile range, minimum and maximum range, and outliers)]. The probability of fledging any young was analyzed using GLM with binomial error structure and logit link function; (N = 438 broods), while the analysis fledgling numbers was based on GLM with normal error structure; N = 369 broods with ≥1 fledgling (see **Supplementary Tables 5, 6** for further details). 95% confidence intervals are presented around lines.

($\chi^2_{1,425} = -12.57$, $P = 0.028$; **Figure 4B**). This interaction between lay date and year arose because the probability of fledging at least some hatchlings declined with increasing lay date in the early-mid phenology years of 2014, 2016, and 2017 (estimate ± SE for these 3 years = -0.044 ± 0.020; $\chi^2_{1,293} = -5.00$, $P = 0.025$), but showed a non-significant tendency for the reverse in the other (mid-late) years (0.10 ± 0.060; $\chi^2_{1,137} = 1.76$, $P = 0.078$). All other interactions were non-significant (**Supplementary Table 5**).

An average of 6.0 nestlings fledged from nests that did not experience complete brood failure (±1.9 *SD*, range: 1–11; **Supplementary Table 6**). Later-breeding nests fledged fewer young than early nests, with 0.08 fewer nestlings fledged per day delay in laying of the first egg ($F_{1,362} = 34.95$, $P < 0.001$). There was no effect of elevation ($F_{1,361} = 0.004$, $P = 0.95$; **Figure 4C**) on the number of fledglings produced, although there was significant inter-annual variation in fledging numbers ($F_{5,362} = 6.71$, $P < 0.001$), ranging from an average of five fledglings in the mid-late year of 2015 to almost seven in the late year of 2013 (**Figure 4D**). There were no significant two-way interactions including lay date, number of eggs incubated, elevation or year (**Supplementary Table 6**).

Nestling Mass

Overall, mean nestling mass in broods between the age of 11–18 days was 10.4 g (±1.0 *SD*), ranging from 5.9–12.8 g (**Supplementary Table 7**). Older broods were heavier than younger broods (linear effect: $F_{1,337} = 11.63$, $P < 0.001$), although age effects tended to asymptote for old broods (quadratic effect: $F_{1,336} = 3.28$, $P = 0.071$). There were no main effects of lay date ($F_{1,335} = 0.37$, $P = 0.54$) or elevation ($F_{1,334} = 0.095$, $P = 0.76$) on nestling mass. There was significant inter-annual variation in nestling mass ($F_{4,337} = 3.60$, $P = 0.0068$), ranging from an average of 10.2 g in the early year of 2017 to 10.7 g in the mid-year of 2014 (**Figure 5A**). Any tendencies for lay date effects on nestling mass to vary among years were driven by outlying late nests (**Supplementary Table 7** and **Supplementary Figure 4**). However, there was a more robust year * elevation interaction ($F_{4,332} = 4.083$, $P = 0.0030$; **Figure 5B**). This interaction was driven primarily by a strong negative association between elevation and nestling mass in 2014, whereas in other years this association was weak or even slightly positive (2015). The interactions between lay date and elevation and between lay date and brood size were not significant, although there was a slight (non-significant) trend for a more positive relationship between nestling mass and lay date with increasing elevation (**Supplementary Table 7**).

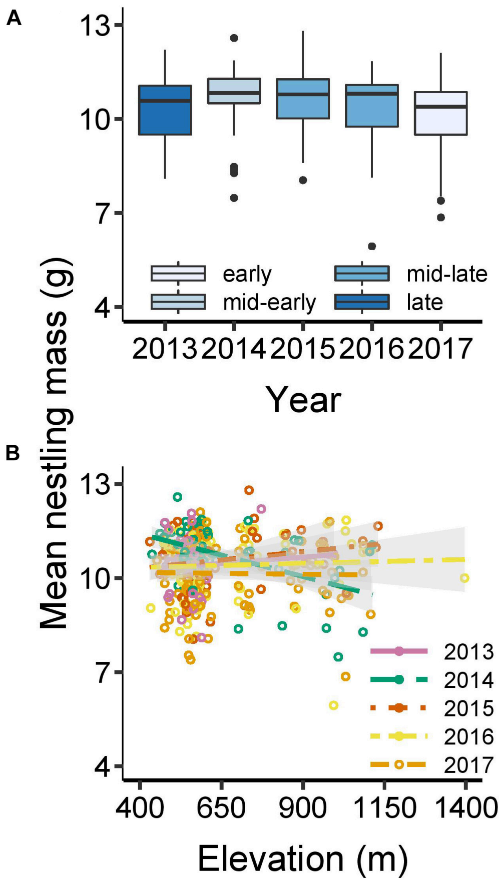

FIGURE 5 | Mean nestling mass (g) as a function of: **(A)** year; and **(B)** the interacting effects of elevation and year. Analyses based on a LM with normal error structure; *N* = 345 broods (see **Supplementary Table 7** for further details). Points show raw values, while predicted lines with 95% confidence intervals control for brood age **(B)**. Boxplots generated from raw data (showing median, interquartile range, minimum and maximum range, and outliers).

DISCUSSION

By combining a multi-year study with an elevational gradient, we were able to investigate a population's capacity for altering breeding phenology across a broad temperature range and the downstream reproductive consequences. Breeding phenology varied markedly among years and especially across the elevational gradient (**Table 2**). In accordance with an assumption of the environmental constraints hypothesis, early phenology, especially at high elevation, was associated with lower and more variable temperatures during breeding. Although early breeders laid larger clutches and fledged more young from successful nests than later breeders on average, we found some evidence to suggest that breeding at low temperatures is associated with reduced success. First, in three of the 6 years the probability of fledging any young was reduced among early breeders, while the number of fledglings produced from success nests was highest in the latest year (2013) and amongst the lowest in the earliest year of our study (2017). Second, both the probability of fledging young and hatching success was reduced at high elevation where temperatures are colder. We have little evidence to suggest that brood failure arose as a result of nest predation nor through reduced food availability. For example, years with high breeding failure did not necessarily have a reduced number of fledglings per successful nest (e.g., 2012, 2013) nor did nestlings have reduced mass (e.g., 2015). Similarly, successful nests fledged the same number of young and at comparable masses across the elevational gradient. Together, our evidence lends support to the hypothesis that the strength of directional selection on advancing phenology can be weakened in small endotherms by an increased probability of experiencing challenging environmental conditions early in the season. This effect could have implications for explaining evolutionary lags between endothermic predators and ectothermic prey.

There is considerable cross-taxonomic support for the suggestion that the phenology of key life events is changing in response to increasing temperatures (Parmesan and Yohe, 2003; Root et al., 2003; Thackeray et al., 2010). However, what is less clear is the degree to which such changes are caused by plastic versus evolved responses, and the limits to advancing phenology (Thackeray et al., 2010; Visser et al., 2015). Long-term studies of tit species breeding in the United Kingdom [1961–2007; (Charmantier et al., 2008) and Sweden (1969–2012; Källander et al., 2017)] have shown advancements of lay date of ca. 14 and 11 days, respectively, in response to 2–3°C increases in maximum spring temperatures. While such changes are doubtlessly caused, in part, by plastic responses to changing temperatures (e.g., Gienapp et al., 2008; Merilä and Hendry, 2014; Phillimore et al., 2016), studies of 40 years on short-lived species, where individuals breed in their first year of life, will also provide sufficient time for evolutionary responses to selection (Sheldon et al., 2003; Charmantier et al., 2008). As a consequence, at least part of the changes in phenology documented in these studies is likely to be a result of evolution (Merilä et al., 2001; Charmantier and Gienapp, 2014; Ramakers et al., 2019). Despite considerable changes in lay date observed over time in such short-lived, temperate, insectivorous passerines, a significant mismatch between the phenology of birds and their prey remains, and it is unclear why birds do not advance lay date more to overcome the detrimental fitness consequences of mismatch (Both et al., 2009a,b; Visser et al., 2012; Radchuk et al., 2019). A better understanding of when and why birds do not (or cannot) breed earlier might be obtained from observations, as presented in our study, in a population experiencing considerable variation in temperature over shorter time periods to avoid 'confounds' of evolutionary responses.

By combining observations across 6 years and a 1,000 m elevational gradient we were able to document variation in breeding phenology over a short time period that complements what we have learned from long term studies. For example, in 2017, laying occurred an average of 9, 19, and 24 days earlier

TABLE 2 | Summary of significant predictors per response variable: lay date, clutch size, probability of hatch failure, fledging success, total number fledging and mean nestling mass per brood.

Response variable	Significant predictors	Estimate	±*SE*	Directionality
Lay date	Elevation	0.025	0.0019	↑
	Year	−8.14–4.86		
	Elevation*year	−0.018–0.017		
Clutch size	Elevation	0.0014	0.00036	↑
	Lay date	−0.072	0.0072	↓
	Year	−0.36–0.74		
Probability of hatch failure	Elevation	0.0015	0.00060	↑
	No. eggs incubated	0.23	0.082	↑
	Year	−1.92–1.54		
Fledging success	Elevation	−0.0022	0.00059	↓
	Lay date*year	−0.19–0.018		
Total number fledging	Lay date	−0.077	0.013	↓
	Year	−1.75–0.031		↓
Average nestling mass per brood	Brood age	0.30	0.089	↑
	Brood size ˆ2	−1.95	0.98	↓
	Year	−0.30–0.48		
	Elevation*year	−0.0036–0.000023		

Normal response variables (lay date, clutch size, total number fledging, mean nesting mass per brood) were analyzed using LMs with normal error structure and non-normal response variables (probability of hatch failure, fledging success) using GLMs with binomial error structure and logit link function. Significance was set at α < 0.05. Estimates and standard errors are provided for continuous terms and ranges of estimates are provided for categorical terms. Directionality of continuous response variables in relation to continuous predictors is provided.

than in 2013 at low, mid and high elevations, respectively, and females at high elevation began laying 11 days later than those at low elevation, on average. This variation is dramatic, and on par with long-term studies spanning decades described above (e.g., Charmantier et al., 2008; Källander et al., 2017). To put this variation in perspective, at the onset of egg-laying in the late year of 2013, pairs in 2017 were already beginning to incubate their ∼9-egg clutches at low elevation, while, at high elevation, they were in the first week of nestling-rearing (because breeding was proportionally earlier at high elevation in that year). That this variation was observed over just a handful of years suggests that changes in breeding phenology over this study are not a consequence of evolution. However, it is conceivable that later breeding across the elevational gradient is a consequence of local adaptation or genetic drift. While evidence for local adaptation has been observed across short-distances in blue tits across contrasting habitat types (evergreen versus deciduous woodland; Porlier et al., 2012), we think genetic differences are unlikely to offer a valid explanation for the marked phenological variation observed in our study. First, all our nest boxes were located in deciduous woodland, with overlap in tree species composition and prey (Lejeune et al., 2019). Second, our low, medium and high elevation woodlots were located within 0.6–16 km of each other in contiguous woodland habitat; well within 1 *SD* of average dispersal distances estimated for this species [mean = 5 km ± 15 (*SD*); Paradis et al., 1998]. Indeed, we have recorded several instances of dispersal between our sites. Finally, although lay date was delayed by an average of 14–19 days at high versus low elevations in five of the years, in 2017 lay date was delayed by just 4 days at high elevation and was sufficiently early in that year to be as early as the second earliest year in low elevation sites (**Table 1**). Thus, pairs in our population, particularly those breeding at higher elevations, would appear to have the capacity to breed considerably earlier than they typically do in most years. The obvious question is why do they not start breeding earlier, particularly given the demonstrated mismatched phenology of such species with peak invertebrate prey during nestling rearing (e.g., Van Noordwijk et al., 1995; Visser et al., 1998, 2003, 2012)?1

The answers to this question are integral to understanding phenological mismatch and are of general importance. While many populations are advancing breeding phenology in response to warming springs (Thackeray et al., 2016), responses are not universal. For example, no systematic change in lay date was observed in a Dutch great tit population studied over more than 20 years (1973–2006), despite spring temperature increasing by up to 2°C over the same time period (Visser et al., 1998; Husby et al., 2010). Indeed, data from 24 European great tit and blue tit populations suggests significant variation in the phenological responses to increasing spring temperatures, even among neighboring populations (Visser et al., 2003). Further, even for those populations that are responding, higher trophic levels are typically responding with reduced magnitude compared with lower trophic levels. The common explanation is that mismatching is due to evolutionary lags of higher trophic levels with longer generation times (Cushing, 1969; Visser and Both, 2005). However, the results of this study (and others, e.g., Visser et al., 2003; Both et al., 2006; Gienapp et al., 2008; Merilä and Hendry, 2014) highlight that the answer is likely to be nuanced, and influenced in significant part by within- and among-year variation in meteorological patterns (Visser et al., 2015). Understanding why our high elevation populations do not advance breeding despite the ability to do so will provide new insights to phenological mismatch in this and other populations.

If an increasing probability of experiencing more challenging environmental conditions acts as a significant constraint on advancing phenology we would expect early breeders to be sometimes disadvantaged (Zając, 1995; Visser et al., 2015). It is well known that unfavorable meteorological conditions at critical times can have significant impacts on organisms, with cascading effects on interacting species (Parmesan, 2006; Marrot et al., 2017). For example, the phenology of budding in many plants is highly sensitive to spring temperatures, with plants being killed by cold snaps (Weiser, 1970). Even though the main prey of blue tits, caterpillars, are relatively cold tolerant (Nadolski and Bañbura, 2010), insectivorous prey are less active during colder conditions, and thus harder to find (Taylor, 1963). However, the degree to which early breeding endotherms are disadvantaged by a return of wintery conditions during breeding is less clear. Nevertheless, in house sparrows (*Passer domesticus*), hatching success was negatively affected by extremely cold days during incubation (Pipoly et al., 2013). Likewise, wintery conditions are known to cause delays to the onset of incubation and hatching and to be associated with reduced reproductive success in Polish great tit and blue tit populations (Kluen et al., 2011; Glądalski et al., 2018, 2020). That blue tits in our population can suffer from challenging meteorological conditions, including early in the season, comes from at least two sources. First, hatching failure was significantly higher in 2012 and 2015, and the former at least had unusually cold weather during egg-laying and incubation of early breeders. Furthermore, early breeders tended to have increased brood failure in 2012, 2013 and 2015 compared with the other years. In these 3 years, early breeders experienced the lowest daily maximum temperatures, while 2012 and 2013 were also the coldest 2 years on average during the month from 20 March. As mentioned above, brood failure is difficult to explain by differences in predation or in prey availability, since clutch sizes, fledgling numbers at successful nests and nestling mass were not reduced in these years compared with the others. Second, hatching failure and complete loss of broods was more common at high elevation where temperatures were significantly colder and more variable during both incubation and nestling periods. Further, if territory quality were inferior at higher elevations *per se*, we would expect reduced clutch sizes, fledgling numbers in successful nests, and/or nestling mass at high elevation nests compared with those at lower elevation, but none was the case. Together these results are consistent with the environmental constraints hypothesis, that challenging weather conditions more often experienced early in the breeding season, weakens the strength of selection on phenological advancement (Visser et al., 2015).

While environmental constraints on early breeding as outlined above should dilute the strength of directional selection on advancing phenology, they were insufficiently strong to alter the shape of the linear seasonal declines in fecundity and fledgling production. Seasonal declines likely exist because early breeders are often better-quality individuals on better quality territories (Verhulst and Nilsson, 2008), but they might also in part be explained by well-documented reductions in prey availability later in the season (Verhulst and Tinbergen, 1991; Winkler and Allen, 1996; Emmenegger et al., 2014). Clarifying the strength of selection on advancing phenology, therefore, requires a better understanding of the associations among temperature, the cues used to time breeding and the timing of prey availability (Visser and Both, 2005). Nevertheless, our results suggest that such associations might be more complicated than is typically assumed. Most notably, whilst we found no significant variation in the strength of seasonal declines (i.e., slopes) in breeding success among years, there were significant among-year differences in average breeding success (i.e., intercepts) which are not obviously driven by phenology. Indeed, many patterns we detected were not consistent with typical patterns where early breeders are more successful. Breeding phenology was advanced at high elevation relative to temperature compared to low elevations, but these earlier breeders did not yield higher fitness than low elevation birds. In addition, we found no evidence for a relationship between breeding phenology and clutch size across years and clutch size was comparable across the elevation gradient, despite later lay dates at higher versus lower elevations. Furthermore, while the probability of fledging young showed seasonal declines in early-mid phenology years, the pattern was reversed in mid-late phenology years. Finally, fledgling numbers at successful nests were comparable across the elevational gradient, despite marked variation in phenology, and were not influenced by the average phenology of a given year [e.g., numbers were highest in mid-early (2014) and late (2013) years, lowest in mid-late 2015 and intermediate in the early year of 2017]. One explanation for these patterns is that the associations among temperature, timing cues and prey availability co-vary non-linearly, leading to inter-annual variation in the association between phenology and prey availability. For example, because the developmental rates of ectothermic invertebrates can be more than halved in favorable temperatures (Buckley et al., 2012) yet are more temperature-invariant in endotherms (Buse et al., 1999), it is likely that phenological mismatches are exacerbated in early compared to later phenology years. Thus, we might expect breeding success in species such as blue tits to be maximal in years where conditions are suitably cold early to slow the development of their prey, but not so challenging to compromise their own success. In other words, the fitness impacts of phenological mismatch could paradoxically be more severe in early years whereas the impact of mismatch might be more limited in later phenology years. Either way, the finding that early phenology years do not associate with increased breeding success will likely act as a further impediment to the evolution of advancing phenology in endothermic predators. Thus, even in the absence of challenging conditions, inter-annual variation in the timing and magnitude of environmental conditions might generate a fluctuating selection pressure on absolute timing; further diluting the strength of selection for advancing phenology in iteroparous organisms and compounding the evolutionary lag across trophic levels.

In conclusion, we propose that short-term studies using elevational temperature gradients within populations provide a valuable complement to long-term studies for understanding population responses to climate variation and change. Most importantly, our approach provides a clearer insight into the capacity for populations of a current genotype to respond to meteorological variation, since we are able to introduce such variation to the same population using an elevational gradient. We found that despite a clear capacity for earlier breeding (based on lay dates in 2017), breeding was typically delayed, particularly at high elevation. It is not known whether earlier breeding would have been more beneficial in any of the sites or years, and so the degree of any phenological mismatch is unknown. However, it is noteworthy that breeding at high elevation and early breeding in some years was associated with increased probabilities of brood failure and there was no obvious association between average phenology in a given location or year and breeding success. Together, these results suggest that challenging environmental conditions during breeding can act as an evolutionary brake on advancing phenology and that environmental variation among years dilutes the strength of any directional selection on advancing phenology across evolutionary timescales. The obvious next step is to elucidate the association between the breeding phenology of tits across years and sites and the patterns of prey availability, as well as to identify the environmental cue that underpins phenology in our population.

Multiple cues likely instigate breeding (Gienapp et al., 2010), and identifying such cues are beyond the scope of this study. Suffice to say that if the cues involve day length and temperature (Lack, 1954; Lambrechts et al., 1996; Dawson et al., 2001; Gienapp et al., 2010; Bonamour et al., 2019), it will need to be an interaction between the two to explain why delayed breeding at higher elevations occurs at reduced temperatures than at lower elevations since our population has the same day length on a given date. In order to advance phenology significantly, it might be that it is selection on and evolution of the cues used to time breeding that need to change (Lyon et al., 2008). This is especially important in light of the increased likelihood of extreme weather events under future climate prognosis (Intergovernmental Panel on Climate Change, 2014), and these extreme weather events should particularly impact early breeders (e.g., Glądalski et al., 2014; Moreno et al., 2015). Further studies from a combination of longitudinal, experimental and environmental cline settings are required to unpack the relative contributions of selection for and against advancing breeding phenology under current climate change, with due consideration of constraints and cues.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

ETHICS STATEMENT

The animal study was reviewed and approved by the state of Ariége animal experimentation review (Préfecture de l'Ariège, Protection des Populations, no. A09-4) and the Région Midi-Pyrenées (DIREN, no. 2012-07). Bird capture was carried out under permits to ASC from the French bird ringing office (CRBPO; no. 13619; PP576).

AUTHOR CONTRIBUTIONS

ACB, ASC, and AFR conceived the study and wrote the manuscript. All authors collected data. ACB compiled the data and conducted the statistical analyses. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.563377/full#supplementary-material

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Timing and Intensity of Weather Events Shape Nestling Development Strategies in Three Alpine Breeding Songbirds

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Across taxa, offspring size traits are linked to survival, and life-time fitness. Inclement weather can be a major constraint on offspring growth and parental care. Despite the adaptive benefits of larger offspring, we have a limited understanding of the effects of severe environmental conditions across developmental stages and how coping strategies differ among species. We assessed the influence of inclement weather on offspring size and mass traits within populations of three alpine breeding songbirds in British Columbia: (1) horned lark (*Eremophila alpestris*), (2) dark-eyed junco (*Junco hyemalis*), and (3) savannah sparrow (*Passerculus sandwichensis*). Specifically, we investigated at which stages during early-life development offspring are most vulnerable to inclement weather and whether thresholds exist in the developmental response to severe weather events. Across species, we identified two critical periods that best predicted offspring size: (1) clutch initiation, and (2) the nestling stage. Colder temperatures experienced by the female during clutch initiation were associated with larger, heavier offspring in horned larks but smaller offspring for savannah sparrows, indicating the potential for maternal effects, albeit acting through different mechanisms. Additionally, horned lark offspring were resilient to colder average temperatures during the nestling stage but were vulnerable to extreme cold events and multi-day storms. In contrast, dark-eyed junco nestlings were robust to storms, but smaller size and mass traits were associated with lower daily maximum temperatures (i.e., more mild temperature challenges). We suggest species differences may be linked to life-history traits, such as: (1) the thermoregulatory benefits of larger body mass in horned larks, (2) the benefits of greater nest cover to buffer dark-eyed junco against precipitation events, and (3) delayed clutch initiation for savannah sparrows to limit exposure to cold storms. We provide evidence for stage-specific impacts of inclement weather on offspring development with implications for reproductive success. These results advance our understanding of early-life resilience to stochastic environments, as we may be able to predict differences in the vulnerability of alpine species to increasingly variable and severe weather conditions.

Keywords: dark-eyed junco (*Junco hyemalis*), extreme weather and climate events, horned lark (*Eremophila alpestris*), cold storms, savannah sparrow (*Passerculus sandwichensis*), sympatric breeding, altricial nestling growth rate, high latitude temperate mountains

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INTRODUCTION

Inclement weather and temperature regimes can strongly influence size and mass development in homeothermic vertebrates (Gillooly et al., 2002; Nord and Giroud, 2020). Since larger offspring size is often associated with greater survival and life-time reproductive success (Marshall et al., 2018), the developmental period represents a prime target for selection to maximize fitness for both offspring and their parents (Rollinson and Rowe, 2015; Vindenes and Langangen, 2015). Altricial songbird development occurs across several well-defined stages: ovum development (internal), egg incubation (external; warmth required), and the nestling stage (warmth and food required). While distinct, these stages are not compartmentalized, as conditions that affect development in one stage can influence subsequent stages (Monaghan, 2008; O'Connor et al., 2014). In addition, songbird offspring are dependent on parental care, such that the development of offspring size traits reflects both parental and offspring responses to prevailing conditions (Auer and Martin, 2017). Inclement weather can stimulate adaptive coping mechanisms in both parents and offspring, reallocating limited resources and promoting or constraining development (Williams, 2012; Wingfield et al., 2017).

Nestlings grow rapidly over a compressed period, such that even short disruptions in growth can negatively influence size at fledging and post-fledging survival (McCarty and Winkler, 1999; Naef-Daenzer and Keller, 1999; Cox et al., 2014). Inclement weather can constrain size trait growth by imposing thermoregulatory challenges that force investment in mass and thermoregulation (Arendt, 1997). Because the physiological and skeletal muscle development required to achieve and maintain endothermy is energetically costly (Price and Dzialowski, 2018), the onset of endothermy and investment in thermoregulation may occur at the expense of size trait growth (i.e., wing length; Olson, 1992; Ricklefs et al., 1994; Węgrzyn, 2013). For example, tree swallow (*Tachycineta bicolor*) nestlings from experimentally heated nests increase wing growth (Dawson et al., 2005), suggesting optimal conditions can release energy allocation constraints and maximize size growth. In addition, weather effects on nestling growth are often linked to food resources, either by altering resource availability or by affecting the ability of parents to capture and deliver food (Stodola et al., 2010; Pipoly et al., 2013; Tuero et al., 2018). As such, altricial offspring are highly dependent on parental investment to mitigate their developmental responses to inclement weather (Auer and Martin, 2017; de Zwaan et al., 2019).

During reproduction, adults must partition resources between parental care and self-maintenance (i.e., survival; van Noordwijk and de Jong, 1986). Resource-challenged individuals may reduce investment in incubation, brooding, or provisioning nestlings in favor of self-preservation activities like foraging; thus, increasing nest exposure to inclement weather (Williams, 2012). Reduced nest attentiveness during incubation can lead to cooled embryos (Coe et al., 2015) and subsequently constrained nestling growth (Nord and Nilsson, 2011; Ospina et al., 2018; Mueller et al., 2019). In addition, environmental conditions experienced by the female during egg formation have the potential to influence offspring size and mass traits through "maternal effects" (Wolf and Wade, 2009; Moore et al., 2019). Challenging environmental conditions can elevate female glucocorticoid levels (e.g., corticosterone), which may flow passively into the developing egg yolk and reduce nestling growth (Love et al., 2005; Saino et al., 2005). Alternatively, if suboptimal conditions are anticipated, females may invest in larger eggs or elevated yolk testosterone levels to increase nestling size, potentially improving offspring resilience to challenging developmental conditions (Mousseau and Fox, 1998; Marshall and Uller, 2007; Bentz et al., 2016). Maternal effects may therefore have particularly important fitness consequences in harsh, variable environments with limited breeding opportunities, and uncertain resource availability (Crino and Breuner, 2015; Kuijper and Hoyle, 2015).

Offspring size traits can be impacted by a broad range of weather events and severities experienced across developmental stages. Developing offspring may be robust to some suboptimal conditions, but exposure to severe, frequent, or prolonged weather events may cross an energy-challenge threshold beyond which constrained development may occur (Cunningham et al., 2013; Wingfield et al., 2017). In stochastic habitats like the alpine, weather conditions fluctuate greatly within and among seasons (Martin et al., 2017), resulting in significant variation in the early-life exposure and timing of extreme weather events among nests even within the same general period (e.g., first clutches). Variable exposure provides the opportunity to pinpoint periods during early-life development where offspring are most susceptible to extreme weather and to identify potential threshold events. Additionally, comparisons among sympatric species can reveal evolved differences in the developmental response to challenging weather which may reflect differences in key life-history traits that regulate offspring exposure to the environment (i.e., nest cover, parental care). When considered in a life-history context, assessing the influence of severe weather events on offspring development within and among species can highlight the capacity for species to respond to the prevailing environment, as well as inform predictions of species vulnerability under increasingly variable climatic conditions.

We investigated the influence of inclement weather on offspring size trait variation within populations of three ground-nesting songbirds breeding in alpine habitats: (1) horned lark (*Eremophila alpestris*), (2) dark-eyed junco (*Junco hyemalis*), and (3) savannah sparrow (*Passerculus sandwichensis*). Specifically, we assessed: (i) the relative effect of temperature and precipitation variables on nestling size traits, (ii) the importance of severity (i.e., extreme weather events), and (iii) how the timing of inclement weather across developmental stages (ova development, incubation, and nestling stage) impacts offspring development. We predicted that all species would respond most strongly to severe weather events like storms and extreme cold (Wingfield et al., 2017). We also expected the strongest effects to occur during the late incubation and early nestling stage when females must balance time on the nest with self-feeding and provisioning nestlings (Nord and Williams, 2015).

Finally, while our three focal species share comparable life-history traits (e.g., ground-nesters, similar development rates), they differ in two key traits that are associated with the thermal environment of the nest and potentially resilience to challenging weather conditions (**Table 1**). Specifically, nest cover and body mass may influence environmental exposure and parental investment requirements. Therefore, we also investigated: (iv) differences among species in relative weather effects across developmental stages. Minimal nest cover for horned larks may make offspring more susceptible to heavy precipitation events, particularly in combination with low temperatures, or "cold storms" (Martin et al., 2017). However, a lower brood mass for dark-eyed junco and savannah sparrows may reduce heat retention within the nest, potentially forcing an earlier investment in the development and maintenance of endothermy while also requiring females to invest more in brooding behavior and less in provisioning offspring (Nord and Nilsson, 2012; Andreasson et al., 2016). A larger body mass may reduce the severity of this trade-off, such that horned larks may be less susceptible to thermoregulatory challenges with a greater capacity to buffer offspring against severe or prolonged weather events (Wendeln and Becker, 1999; McNamara et al., 2004).

MATERIALS AND METHODS

Focal Species

We studied high elevation populations of horned lark, savannah sparrow, and Oregon dark-eyed junco (*J. h. oreganus*) in British Columbia, Canada. Horned larks are open-country songbirds that breed in sparsely vegetated habitats such as short-grass prairies, desert, and tundra from 0 to over 4,000 m above sea level (a.s.l.; Beason, 1995). Savannah sparrow are also open-country specialists that inhabit cultivated fields, meadows, and alpine tundra >2,000 m a.s.l. in British Columbia (Ryder, 2015), but, unlike horned lark, associate with taller grasses and shrubs (e.g., *Salix* sp.; MacDonald et al., 2016). Dark-eyed junco breed in open-forest and shrub-dominated habitats from 0 to 3,775 m a.s.l. (Nolan et al., 2002).

For these species, alpine populations predominantly raise one complete brood per season, with evidence for occasional double brooding (Bears et al., 2009; Martin et al., 2009;

TABLE 1 | Comparison of select life-history traits among horned lark, dark-eyed junco, and savannah sparrow which may contribute to differences in the thermal environment of the nest and offspring resilience to prevailing weather.

	Horned lark	Dark-eyed junco	Savannah sparrow
Nest			
Nest cover	16 ± 18% (0–80%)	98 ± 3% (90–100%)	70 ± 20% (21–100%)
Surrounding substrate	Often tuft of grass/heather behind nest.	Often under overhang (shrub, rock, bank).	Thick, tall grass or other vegetation.
Nest contents			
Brood size	3.7 ± 0.7 (1–5)	4.3 ± 0.6 (3–6)	4.1 ± 1.0 (2–6)
Incubation period (d)	12.2 ± 0.8 (10–15)	13.1 ± 0.4 (12–14)	12.5 ± 1.0* (9–15)
Nestling period (d)	9.1 ± 1.2 (7–13)	11.4 ± 1.5 (7–15)	10.9 ± 1.0* (8–13)
Parental care			
Incubation	Female. No mate feeding.	Female. No mate feeding.	Female. No mate feeding.
Brooding	Female	Female	Female
Nest provisioning	Biparental	Biparental	Biparental
Primary nestling food*	Lepidoptera larvae Coleoptera larvae Assorted arthropods Seeds (early season)	Assorted arthropods Larvae of all orders.	Lepidoptera larvae Tenthredinid larvae Assorted arthropods Berries
Adults			
Adult body mass (g)	34.1 ± 2.0 (29.0–39.9)	18.0 ± 1.1 (16.2–21.6)	18.2 ± 2.6 (16.0–26.5)
Adult food*	Arthropods Seeds	Arthropods Seeds	Arthropods Seeds

*Nest traits are based on 616 nests for horned lark, 76 for dark-eyed junco, and 89 for savannah sparrow. Adult mass values were taken from 106 horned larks, 82 dark-eyed juncos, and 23 savannah sparrows. Values are the mean ± standard deviation with the range in brackets. All traits are derived from the populations addressed in this study unless marked by an asterisk. Nest cover was measured immediately after nest completion (MacDonald et al., 2016; de Zwaan and Martin, 2018). *Combines personal observation with information from Birds of the World (Billerman et al., 2020). Specifically, horned lark (Beason, 1995), dark-eyed junco (Nolan et al., 2002), and savannah sparrow (Wheelwright and Rising, 2008).*

Camfield et al., 2010). Horned lark and dark-eyed junco begin initiating clutches by mid-May, while savannah sparrows initiate later, from early- to mid-June (Bears et al., 2009; Martin et al., 2017; de Zwaan et al., 2019). Females of each species lay one egg a day and usually begin incubation on the penultimate egg (Beason, 1995; Nolan et al., 2002; Wheelwright and Rising, 2008). See **Table 1** for more details on nest traits, development rates, and parental care.

Study Sites

We studied savannah sparrows from 2003 to 2004 and horned larks from 2015 to 2018 in approximately 4 km^2 of subalpine and alpine habitat on Hudson Bay Mountain (HBM) near Smithers, British Columbia, Canada (54.8°N, 127.3°W; **Figure 1**). Savannah sparrows nested primarily between 1,500 and 1,800 m a.s.l. in both alpine tundra and open sub-alpine habitat consisting of scattered krummolz subalpine fir (*Abies lasiocarpa*) and willow shrubs (*Salix* sp.) interspersed with alpine meadows. Horned larks nested entirely above treeline from 1,650 to 2,000 m a.s.l. This site is characterized by high winds and fluctuating temperatures (Camfield and Martin, 2009). Snowmelt varies considerably but often extends into mid-June, resulting in compressed breeding seasons (Camfield et al., 2010).

From 2013 to 2015, we studied Oregon dark-eyed juncos between 1,900 and 2,200 m a.s.l. on Mount Mackenzie near Revelstoke, BC, Canada (51.0°N, 118.2°W; **Figure 1**). This habitat is considered predominantly subalpine, including stands of Engelmann spruce (*Picea engelmannii*) and subalpine fir with patches of transitional alpine meadows and tundra. Snowmelt occurred from June to early July, slightly later than at HBM. This is likely because seasonal precipitation was considerably greater at Mount Mackenzie over the study period coupled with colder early-season temperatures (**Table 2**). Otherwise, climate conditions were comparable between sites, particularly the extensive within and among year variability (**Table 2**).

Field Methods

For all species, nests were located by systematic territory searches and behavioral observation. Nests were monitored every 2–3 days except for near hatch and fledge when we switched to daily nest visits. At 7-days post-hatch (day 0 = hatch date), we measured wing length (±0.5 mm), tarsus length (±0.02 mm), and mass (±0.01 *g*). For savannah sparrows, only tarsus length and mass were measured. Junco nestlings were measured every 2 days starting at hatch; however, we limited our consideration to measurements at 7-days for this study to allow for comparisons among species. Infrequently, nestlings were measured at 6- or 8-days post-hatch, and thus we also recorded age of measurement to control for this variation. Each nestling was banded with one United States Geological Survey (USGS) numbered aluminum band and 2–3 plastic color bands for subsequent identification.

Weather Data

Hudson Bay Mountain

Precipitation and temperature variables were recorded using two HOBO weather stations (Onset Computer Co., Pocaset, MA, United States): (1) a U30-NRC station for 2015 and 2016, and (2) an RX3000 satellite station for 2018. Both stations were located at 1,695 m a.s.l., within 1.2 km of all nests, and should therefore be representative of ambient conditions within the observed elevational ranges of both species (horned lark: 1,650–2,000 m; savannah sparrow: 1,500–1,800 m). Temperature sensors were positioned approximately 3 m above ground. Raw weather data were recorded every 4 min and then averaged hourly.

Precipitation data were missing for 2003 and 2004 (savannah sparrows), and both temperature and precipitation data were missing for parts of 2017 (horned lark). To estimate precipitation for these periods, we used values from the Smithers Regional Airport ~8 km from our site (station ID = SA10774981; elevation = 522 m). Total precipitation was poorly correlated between stations, but station SA10774981 correctly identified days on HBM with or without precipitation 81% of the time and days with ≥10 mm of precipitation 90% of the time (Martin et al., 2017). Therefore, to be consistent across all years, whether exact precipitation amounts were available or not, we classified each day as a precipitation day (≥1 mm) or storm event (≥10 mm) using a binomial 0 or 1. To estimate missing temperature values, we interpolated hourly estimates of air surface temperature from the 8 nearest grid points in the National Centers for Environmental Prediction (NCEP) R-1 dataset using the R package "RNCEP" (Kemp et al., 2012). Comparisons of the interpolated estimates with existing measurements from the study site were highly correlated (r_p = 0.91), validating this method. We regressed recorded temperatures at HBM on interpolated temperature for all years with existing data (2003–2018) in order to correct for elevational effects. The resulting equation was used to convert interpolated temperature to better align with true temperature measurements:

$$\text{Hudson Bay Mountain} = -1.78 + 1.06\ (\text{interpolated data})$$

Mount Mackenzie

For 2013 and 2014, we used hourly temperature data from a weather station owned by the local ski resort (Revelstoke Mountain Resort, Inc) situated at 1,950 m a.s.l. within our study site (dark-eyed junco elevation range = 1,900–2,200 m a.s.l.). Temperature data were missing for 2015, so we retrieved hourly recordings from a nearby station located at 1,850 m a.s.l. on neighboring Mount Revelstoke (~8.5 km from Mount Mackenzie), part of the Provincial Snow Survey Network (station ID: 2A06P; B.C. Ministry of Environment and Climate Change Strategy 2019). Values from the two sites were highly correlated in 2013 and 2014 (r_p = 0.98) but differed by an intercept, so we used the following equation for conversion:

$$\text{Mount Mackenzie} = -3.53 + 1.12\ (\text{station 2A06P})$$

We also extracted precipitation values from station 2A06P as precipitation data were not available from the ski resort weather station at our site. We compared station 2A06P values to those from the Revelstoke airport (WMO station ID: 1176745), located ~3.5 km from our study site but at 445 m in elevation. While total precipitation correlated poorly, recorded precipitation and storm events matched for 90% of days during the breeding season. Since station 2A06P is at approximately the same elevation as our study

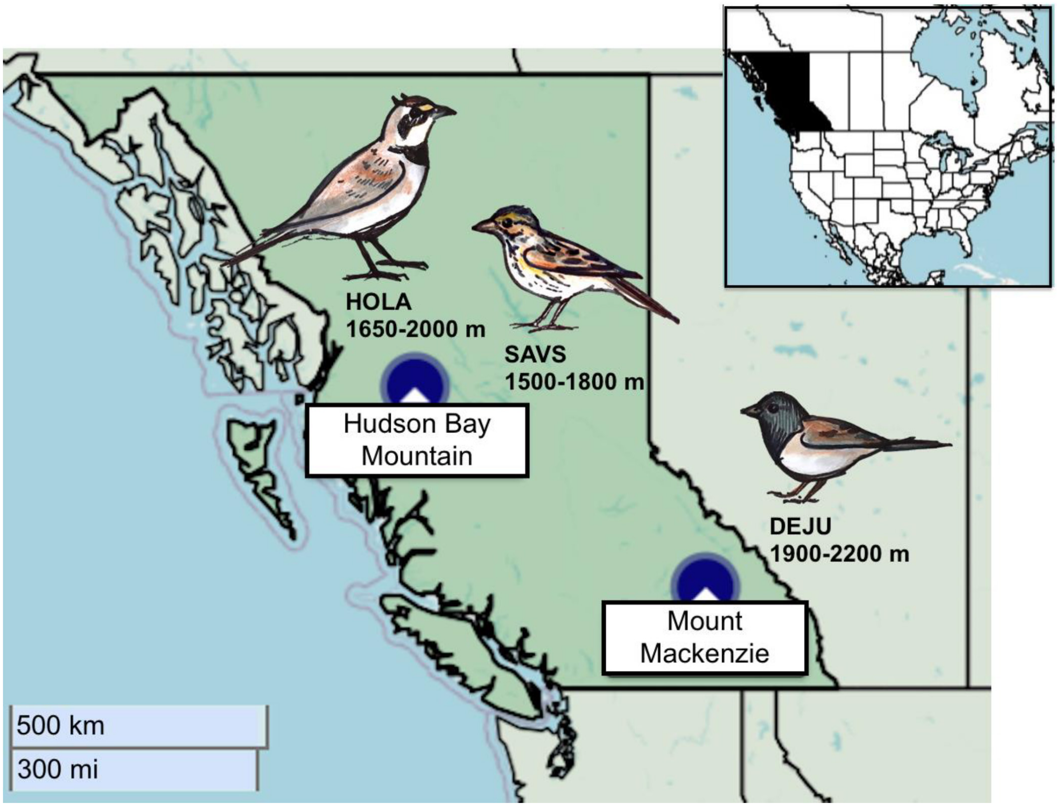

FIGURE 1 | Map of the two alpine study sites within British Columbia, Canada: Hudson Bay Mountain, and Mount Mackenzie. Each study species is associated with the site and elevational range where they were studied. Data were collected for savannah sparrow from 2003–2004, horned lark from 2015–2018, and dark-eyed junco from 2013–2015. Maps: Leaflet JavaScript library with base map and data from OpenStreetMap contributors. Illustrations: A. Drake.

TABLE 2 | Monthly weather variables for each breeding season and study site.

Hudson bay	Temperature (°C)			Precipitation (mm)			
Year	May	June	July	May	June	July	Total
2003^{S}	0.0 ± 3.2	4.8 ± 2.6	8.1 ± 2.8	20	69	56	145
2004^{S}	0.8 ± 2.2	7.2 ± 5.0	9.9 ± 2.5	16	74	40	130
2015^{H}	5.0 ± 4.0	8.3 ± 3.4	9.6 ± 4.3	30	24	46	100
2016^{H}	3.5 ± 3.1	6.7 ± 3.5	8.9 ± 2.9	20	48	83	151
2017^{H}	1.9 ± 2.9	5.0 ± 2.7	7.7 ± 2.1	90	57	31	178
2018^{H}	4.6 ± 3.8	5.7 ± 5.9	11.3 ± 4.9	23	27	22	72
Average	2.6 ± 3.8	6.3 ± 4.2	9.3 ± 3.6	33	50	46	129
Mackenzie	**Temperature (°C)**			**Precipitation (mm)**			
Year	**May**	**June**	**July**	**May**	**June**	**July**	**Total**
2013^{D}	0.9 ± 3.7	3.2 ± 2.5	9.5 ± 3.5	90	140	8	238
2014^{D}	−0.2 ± 3.1	3.1 ± 2.1	9.8 ± 4.0	133	76	85	294
2015^{D}	1.8 ± 3.8	7.3 ± 4.5	9.1 ± 4.1	54	89	82	225
Average	0.8 ± 3.6	4.5 ± 3.7	9.5 ± 3.8	92	102	62	252

Temperature values are the mean ± standard deviation, while precipitation represents the total sum. Superscript letters indicate that the weather variables are associated with savannah sparrows (S), horned lark (H), or dark-eyed junco (D).

site and displays high concordance with weather patterns within the proximate region, we concluded that its precipitation data accurately represented conditions experienced at our study site.

Due to the use of multiple weather stations, we restricted the weather variables we considered to five for which we had a high degree of confidence and that were comparable among study sites: (1) average daily temperature, (2) daily hours ≤10°C, (3) daily hours ≤5°C, (4) precipitation days (≥1 mm/day), and (5) storm events (≥10 mm/day). Daily hours below the 10°C and 5°C threshold reflect cumulative temperature challenges for developing eggs and young. In larks, 10°C is an ecologically relevant threshold, below which females increase incubation efforts (MacDonald et al., 2014) and, during the nestling stage, can prolong offspring development (de Zwaan et al., 2019). However, species or individuals may vary in their ability to respond to moderate temperature thresholds like 10°C, so we also considered hours ≤5°C to address more extreme conditions that may have pronounced effects on early-life development (Pérez et al., 2016). Daily average temperatures were calculated as the average of each day between dawn and dusk (0400–2200 h) to reflect the period when nest contents were most likely to be exposed to ambient temperatures, as night-time incubation attentivity is >90% (Camfield and Martin, 2009). Hours below 5 and 10°C were the sum of hours below each threshold within the same exposure period.

Statistical Analysis

To assess the influence of weather on offspring development and identify the most critical time periods across early-life stages (clutch initiation, incubation, and nestling stage), we used a two-step process. First, for each candidate weather variable, we used a sliding window sensitivity analysis to identify the time periods where each variable showed the strongest relationship with nestling size. Then, for each size trait (wing length, tarsus length, and mass), we fit a global General Additive Mixed-effects Model (GAMM) which included all selected weather variables. Penalized regression splines allowed us to examine non-linear associations between weather variables and size traits within a modeling framework that reduced weather variables to linear effects or dropped them entirely from the model where added complexity did not contribute to overall fit. All weather variables were standardized to allow comparisons among traits and species. All analyses were conducted in R 3.6.3 (R Core Team, 2020).

Sliding Window Analysis

Sliding window approaches systematically test associations between weather metrics and biological variables of interest across all possible time windows within a specified period, and then rank each subsequent model with Akaike Information Criterion (AIC; van de Pol and Cockburn, 2011; van de Pol et al., 2016). With nestling size traits as the response variables, we built models that assessed all windows within a 30-day period prior to nestling measurement at 7-days post-hatch for each nest. This time period encompasses the incubation and nestling stage, as well as, an average of 8–10 days prior to clutch initiation for each species. For many songbirds, ova development takes approximately 3–5 days when nutrients and hormones are transferred from female to offspring (Williams, 2012). Therefore, 8–10 days prior to clutch initiation should be sufficient to capture the ova development period across species. We constrained the tested time windows to a minimum of 3 days and a maximum of the full 30 days. The minimum window was chosen to avoid spurious correlations with single weather events and to allow for weather patterns prolonged enough to stimulate physiological and behavioral responses in females and nestlings.

For temperature variables (average daily temperature, hours ≤5°C, and hours ≤10°C), we calculated the mean, minimum, and maximum values, as well as the variance across all days within each time window. This allowed us to evaluate the relative influence of average conditions, extremes or variability on nestling size and mass traits. For precipitation variables (precipitation days, storm events), we calculated the sum and variance within each time window to assess cumulative effects and variability, respectively.

For each weather variable, all possible time windows were ranked using AIC relative to the null model. The null model included age of measurement, brood size, and clutch initiation date as fixed effects, and nest ID as a random effect to account for non-independence among nestlings of the same nest. The top time windows were chosen based on the lowest AIC if it was a significantly better fit than the null (ΔAIC < –2). If more than one window occurred within 2 AIC of the top window, the one with the strongest β-coefficient was chosen. If distinctly different time windows occurred within the top models (e.g., 30–20 and 7–0 days), then both windows were selected for that weather variable. Due to the large number of comparisons inherent to sliding window approaches, we additionally ran each model on 100 randomized datasets to determine the likelihood of selecting the same top models by chance (Type 1 error; van de Pol et al., 2016). Only weather variables where the observed results were different from the randomized analyses ($P < 0.10$) were selected as candidate variables. An α-value of 0.10 was used at this stage as a conservative approach to maximize the number of candidate variables retained for model selection (see next section). The sliding window analysis was conducted using R package "climwin" (Bailey and van de Pol, 2015).

Model Structure and Selection

For each size trait, we used all selected candidate weather variables to build a global GAMM using the "mgcv" package (Wood, 2011). Age at measurement, brood size, and clutch initiation date were included as covariates in each model, with nest ID as a random effect. For each weather variable, we fit thin-plate regression splines with a maximum of 3 possible knots to test for potential non-linear associations. Models were fit using Restricted Maximum Likelihood (REML) and incorporating penalties for both smoothing factors and the null space. Based on the fit to the data, this process determines whether a variable should be a smoothed term (2 or 3 knots), a linear term, or be removed from the model (Wood, 2003). Variables were removed from the model if their estimated degrees of freedom (edf) were less than 0.7, retained as a linear term between 0.7 and 1.7, and retained as a smoothed term if greater than 1.7. If all weather variables were linear, a linear mixed-effects model was fit to the selected model structure using "lme4" (Bates et al., 2015). We evaluated collinearity among linear terms using the Variance Inflation Factor (VIF) and retained weather variables with a VIF < 3. Standardized β-coefficients were extracted as effect sizes and associations were considered significant if the 95% confidence interval did not include zero.

Data and R code are available from the Figshare Digital Repository: data http://doi.org/10.6084/m9.figshare.13070276 (de Zwaan et al., 2020a); R code http://doi.org/10.6084/m9.figshare.13070267 (de Zwaan et al., 2020b).

RESULTS

We measured 361 horned lark, 120 dark-eyed junco, and 96 savannah sparrow nestlings from a combined 170 nests. At 7-days post-hatch, horned lark nestlings were considerably larger and heavier than dark-eyed junco and savannah sparrow (**Table 3**). First nests for horned lark and dark-eyed junco were initiated at approximately the same time (mid-May) and had a breeding season length of about 50 days (first to last clutch initiation date; **Table 3**). Savannah sparrows began breeding nearly 3 weeks later than larks, resulting in a breeding season that was >50% shorter (**Table 3**). During the 30-day period prior to nestling measurement, horned larks experienced colder temperatures but fewer storms and precipitation days, while dark-eyed junco and savannah sparrow experienced comparable weather conditions (**Table 3**).

Sliding Window Selection of Weather Variables

Across species, the sliding window analysis identified two general time periods where weather influenced offspring development: (1) from several days before clutch initiation to early incubation (approximately 30–16 days prior to nestling measurement at 7-days post-hatch), and (2) the nestling stage (7–0 days; **Figure 2**). The type of weather variable operating within these time windows and extent of its influence differed among species and size traits (Appendix S1: **Supplementary Table 1**). Neither temperature nor precipitation variance were selected in any of the top time windows, suggesting offspring development was not impacted by weather variability itself. Rather, depending on the species, offspring size and mass traits responded most strongly to the average or extreme temperatures within a given window, as well as the cumulative effects of precipitation and storm events (**Figure 2**). When both average daily temperature and hours ≤10°C were selected, they occurred within the same time window and were strongly correlated ($r_p > 0.90$). Thus, we hereafter report only daily temperature as an indicator of mild temperature effects and hours ≤5°C to reflect periods of extreme cold.

Temperature Effects

Average daily temperatures, particularly the coldest day prior-to and during the clutch initiation period (27–16 days prior to measurement), as well as extreme cold (hours ≤5°C) during the nestling stage (7–0 days) were the most influential temperature predictors for the development of size and mass traits in lark nestlings (**Figure 3**). There was a negative relationship between multi-day average temperatures near clutch initiation and wing length (β = −2.6, 95% confidence interval = –4.2, –0.9) and mass (β = −1.2, 95% CI = −2.0, −0.3), such that colder average temperatures were associated with larger and heavier nestlings (**Figure 4A**). During this period, the minimum average daily temperature (coldest day) was also negatively associated with mass (β = −1.5, 95% CI: −2.1, −0.8), and in fact, was a better predictor compared to the multi-day average (ΔAIC = −8.6). Thus, cold days during clutch initiation were associated with heavier nestlings. In contrast, at the nestling stage, an increase in the number of hours ≤5°C was linked to smaller nestlings across all size and mass traits (**Figure 4B**).

For dark-eyed juncos, only temperatures during the nestling stage (7–0 days prior to measurement) were associated with size and mass traits (**Figure 3**). However, unlike larks which responded to periods of extreme cold (hours ≤5°C), dark-eyed junco nestlings responded most strongly to changes in the maximum average daily temperature (warmest day), or an upper temperature limit (**Figure 3**). A warmer maximum during the nestling period was linked to greater wing length (β = 2.5, 95% CI = 1.5, 3.5), tarsus length (β = 0.8, 95% CI = 0.4, 1.1), and mass (β = 0.7, 95% CI = 0.1, 1.0) at 7-days post-hatch (**Figure 4C**).

For savannah sparrows, nestling size trait development was linked to average daily temperatures prior to clutch initiation (30–23 days prior to measurement; **Figure 3**). Greater temperatures were associated with longer tarsi (β = 0.7, 95% CI = 0.2, 1.2; **Figure 4D**), but there was no effect on mass.

Precipitation Effects

Horned lark nestlings responded most strongly to storm events during the late incubation and nestling periods. Greater frequencies of storms 12–2 days and 20–2 days prior to measurement were associated with reduced wing and tarsus length, respectively. However, there was no evidence that storm frequency influenced mass (**Figure 3**). Importantly, only multiple storm events during this time period influenced size trait development, as there was no observable response to a single storm, indicating a possible resilience threshold (**Figure 5A**).

In contrast, changes in dark-eyed junco nestling size traits (wing, tarsus) were not associated with storm events (**Figure 3**). A model that included storms during the nestling stage (5-0 days) had similar support to the top mass model (ΔAIC = 1.8); however, the observed negative trend was not significant for either single (β = −0.3, 95% CI = −1.3, −0.7) or multiple storm events (β = −0.4, 95% CI = −1.7, 1.0; **Figure 5B**).

Savannah sparrow size trait development was also not associated with storms. Instead, a greater frequency of precipitation days prior to clutch initiation and during early incubation (30–12 days) was associated with greater nestling mass (β = 1.8, 95% CI = 1.1, 2.5; **Figure 3**). During this period, precipitation days and average daily temperature were highly correlated ($r_p = 0.72$) and in the absence of precipitation, greater temperature was positively associated with mass (β = 0.9, 95% CI = 0.2, 1.2). Therefore, while precipitation was the better predictor, it was not possible to separate the influence of

TABLE 3 | Nestling size traits at 7-days post-hatch, clutch initiation date, and weather conditions experienced over the 30-day window of each individual nesting attempt across species.

Variables	Horned lark	Dark-eyed junco	Savannah sparrow
	***n* = 361 (110)**	***n* = 120 (35)**	***n* = 96 (26)**
Nestling size traits			
Wing length (mm)	39.1 ± 7.2	29.2 ± 5.1	
Tarsus length (mm)	19.6 ± 1.7	18.6 ± 1.6	18.7 ± 1.6
Mass (g)	20.6 ± 3.6	12.4 ± 1.8	13.8 ± 2.1
Clutch level traits			
First egg*	162 ± 13	175 ± 13	170 ± 8.5
	(138–189)	(142–194)	159–188
Weather			
Avg temp (°C)	6.7 ± 2.4	7.9 ± 2.0	7.7 ± 1.1
	(3.2–10.9)	(3.1–10.2)	(5.1–9.3)
H ≤ 10°C	13.8 ± 3.0	11.0 ± 1.8	12.9 ± 2.3
	(8.0–17.8)	(9.5–16.2)	(10.5–17.6)
H ≤ 5°C	7.4 ± 3.7	6.5 ± 2.7	5.1 ± 1.9
	(2.2–13.7)	(3.3–12.7)	(2.0–9.5)
Storm events	1.1 ± 0.8	2.0 ± 1.3	1.8 ± 0.8
	(0–3)	(0–5)	(1–3)
Precipitation days	8.3 ± 2.8	12.5 ± 3.8	13.2 ± 1.2
	(4–15)	(4–19)	(10–15)

*Values are the mean ± standard deviation. Sample size depicts number of nestlings and nests in brackets. For clutch level traits and weather, values in brackets represent the range. First egg is the average clutch initiation date for the entire breeding season in Julian days, including first nests and re-nests, and the range is the earliest and latest initiated nest across years to depict breeding season length. Temperature hours indicate the average number of hours per day (see Methods for further details). *Julian date: May 1 = 121.*

precipitation and temperature on nestling mass development for savannah sparrows during this period. See Appendix S1: **Supplementary Table 2** for full model outputs.

DISCUSSION

We identified two general periods where offspring size traits were most influenced by inclement weather: (1) clutch initiation, and (2) the nestling stage. We demonstrated greater resilience to cold temperature challenges in horned lark, but also greater susceptibility to precipitation events than in dark-eyed junco and savannah sparrow; particularly the cumulative effects of multiple storms. Further, both horned larks and savannah sparrows exhibited relatively strong associations between temperature during the clutch initiation process and offspring development, indicating the potential influence of maternal effects. By considering differences among species in a life-history context, our results may be generalizable to other alpine breeding species, allowing us to predict how an increasingly variable and extreme climate may influence reproductive success in alpine bird populations.

Temperature Effects During the Nestling Stage

Cold temperatures can constrain nestling size growth (Dawson et al., 2005), with variation in response to cold among species and populations potentially reflecting differences in nestling resource allocation or parental investment (Eeva et al., 2002; Mainwaring and Hartley, 2016; Auer and Martin, 2017). While colder temperatures during the nestling stage were associated with smaller offspring size traits in horned larks, this effect was only expressed during extended periods of extreme cold (hours ≤5°C), indicating general resilience to alpine weather conditions. In contrast, dark-eyed junco nestlings exhibited reduced growth in response to colder daily average temperatures (i.e., more moderate temperature challenges). Nestling horned lark at 7-days post-hatch were nearly 66% heavier than dark-eyed junco (**Table 3**) and therefore may be better able to conserve heat and delay the onset of endothermy to invest in size trait development, even under suboptimal conditions (Calder, 1984; Węgrzyn, 2013; Andreasson et al., 2016). The larger body mass of adult horned lark compared to dark-eyed junco (**Table 1**) may also provide female larks with greater energy reserves, allowing them to brood longer and at colder temperatures and making them better able to buffer their offspring against prevailing conditions (Wendeln and Becker, 1999; Nord and Williams, 2015).

Interestingly, nestling dark-eyed junco size and mass traits were best predicted by the warmest daily average temperature during the nestling stage (i.e., changes in exposure to the upper thermal range). The ability for adult birds to capture prey and provision nestlings should increase with insect activity (Avery and Krebs, 1984). In cold, seasonal environments like the alpine or arctic, daily fluctuations in insect activity and offspring provisioning rates are likely closely linked to ambient temperatures (Low et al., 2008; Tulp and Schekkerman, 2008).

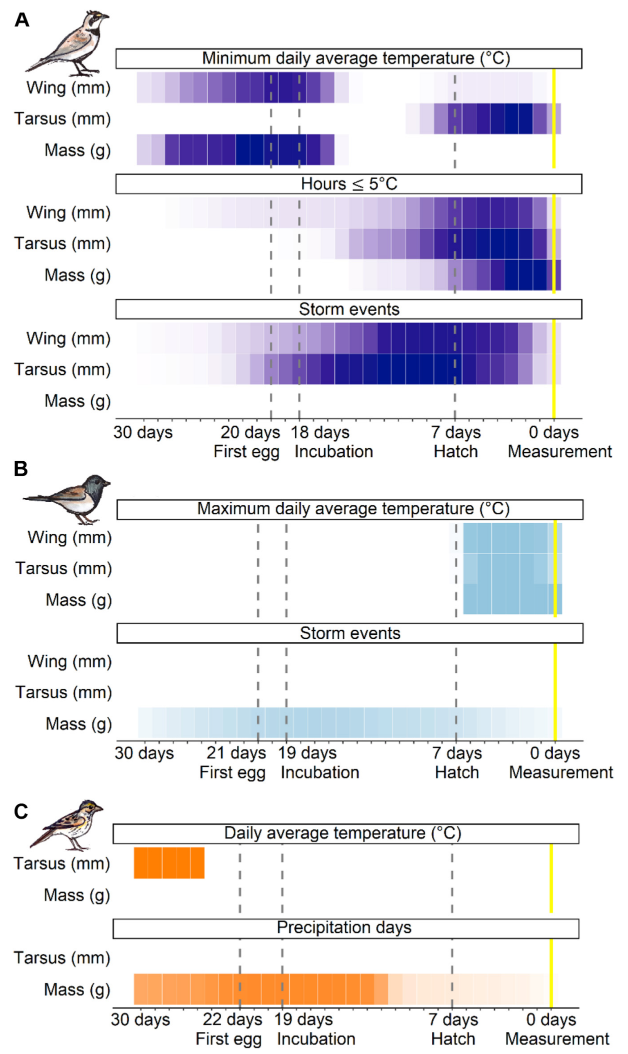

FIGURE 2 | Sliding window results for the top temperature and precipitation variables that influence offspring development across developmental stages for horned lark (**A**; purple), dark-eyed junco (**B**; light blue), and savannah sparrow (**C**; orange). Only traits that passed the randomization test and time windows that had a better fit than the null (≤ 2AIC) are included. Each cell represents 1 day. A darker color intensity indicates greater support for an association between the weather variable and size trait, or a greater number of models that selected that time window.

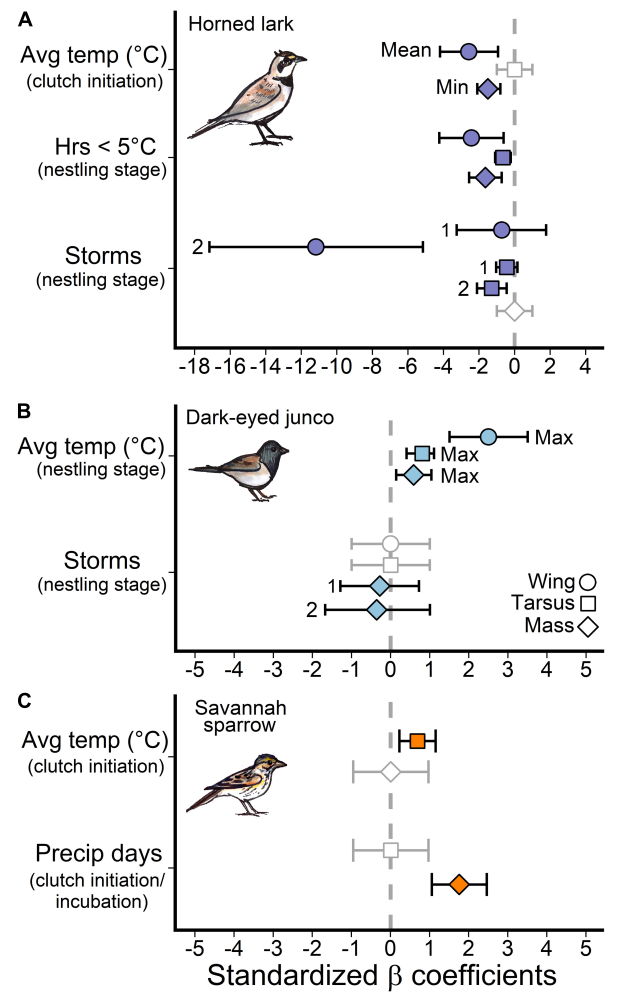

FIGURE 3 | Standardized model effect sizes for temperature and precipitation weather variables for each species. The approximate windows in brackets (clutch initiation, incubation, and nestling stage) are generalizations to facilitate comparisons among species and size traits. Error bars depict 95% confidence intervals and an effect is considered significant if the error bars do not overlap zero (gray dashed line). Mean, min and max labels indicate whether it was the average daily temperature, minimum daily average, or maximum daily average within the selected window that best predicted the size trait. The "1" or "2" labels mark the effect for one storm over the time window or two storms relative to zero storms. Gray points with an effect size of zero and standard deviation of 2 indicate the variable did not pass the sliding window randomization test and therefore was not a candidate variable for model selection.

Therefore, maximum daily average temperature experienced during the nestling stage may reflect an ecological signal of elevated insect activity and thus offspring food availability, with benefits for nestling growth. Additionally, dark-eyed junco nests have greater cover than both horned lark and savannah sparrows (**Table 1**). Greater nest cover offers better concealment from predators, but at the expense of a colder microclimate (Marzluff, 1988; de Zwaan and Martin, 2018). Temperature extremes, like higher maximum temperatures, may be more representative of reduced thermoregulatory challenges for offspring in nests with less sun exposure. Ultimately, detailed information on temperature-specific nestling diet or nest microclimate dynamics among species is required to address these possible mechanisms.

There was no association between temperature during the nestling stage and offspring size traits in savannah sparrows. This is surprising given their previously documented higher nest mortality during periods of suboptimal weather (Martin et al., 2017). However, because the earliest savannah sparrow nests were initiated nearly 3 weeks later than both horned lark (sympatric breeder) and dark-eyed junco, the minimum average temperature experienced during any savannah sparrow nesting

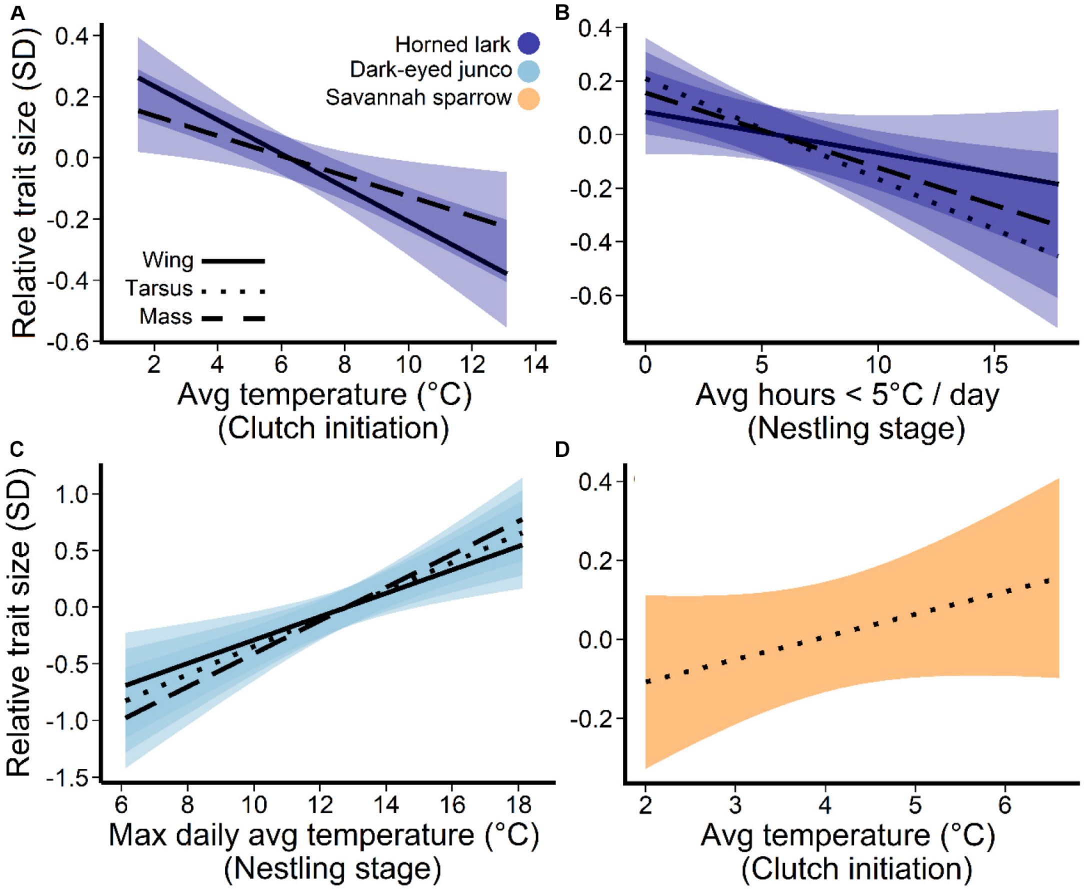

FIGURE 4 | Temperature associations for horned lark, dark-eyed junco, and savannah sparrow. Panels depict **(A)** daily average temperature prior-to and during the clutch initiation period (27–16 days prior to measurement date), **(B)** periods of extreme cold during the nestling stage (7–0 days), **(C)** the maximum daily averages during the nestling stage for dark-eyed junco, and **(D)** average clutch initiation temperatures for savannah sparrows. Lines represent the predicted trends from the linear mixed effects models, controlling for variation within nests, and the shaded areas are 95% confidence intervals of the partial residuals. All response axes represent relative trait size, where zero indicates the mean value and a 1-unit change equals 1 standard deviation.

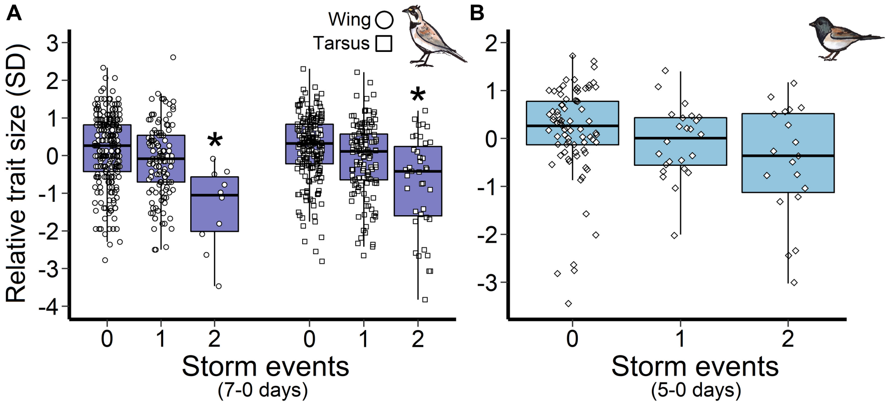

FIGURE 5 | Influence of storm events during the nestling stage on **(A)** horned lark wing and tarsus length, and **(B)** dark-eyed junco mass. Points represent the raw data points and an asterisk indicates a significant difference from zero storms. The scaled trait length was standardized such that each unit is one standard deviation change from the mean at zero.

attempt was significantly higher (**Table 3**). Martin et al. (2017) proposed that this delayed onset of breeding was a potential strategy for savannah sparrow to avoid cold storms and reduce the probability of nest failure. Our results indicate that the warmer temperatures associated with later breeding may also benefit offspring development.

Storm Thresholds and Precipitation Effects

While there was no observable influence of a single storm, multiple storms during the nestling stage constrained offspring growth in horned larks. This aligns with the concept of multiple or cumulative stressors where individuals may be resilient to suboptimal conditions up to a specific threshold (allostasis; Wingfield et al., 1998). We found no storm effect for dark-eyed junco, suggesting they may be more robust to precipitation events. Horned larks have highly exposed nests (16% mean overhead cover) compared to dark-eyed junco (90–100%) where nests were often dug into the bank with an earthen or rock overhang (**Table 1**). Nest placement may therefore underlie differences between species in their susceptibility to storms. Horned lark females brood their nestlings immediately upon onset of rain or snow and remain on the nest for the duration of the weather event, relying on the male to provision nestlings; thus reducing total provisioning rate by at least one half (Goullaud et al., 2018). Prolonged storm events likely impose a significant constraint on nestling food intake and ultimately negatively impact growth rate. For dark-eyed juncos, greater nest cover may make brooding less critical to protecting offspring against precipitation, enabling parents to maintain provisioning rates.

For savannah sparrows, storm events did not influence offspring mass or size traits, despite cold storms being particularly detrimental to their nest success (Martin et al., 2017). Breeding later in the season may not reduce the number of storms birds experience, but it would limit exposure to the more energetically taxing "cold storm" events (Martin et al., 2017; Wingfield et al., 2017). Additionally, we found that warm precipitation prior to and during incubation positively influenced nestling mass in savannah sparrows. While precipitation during the nestling stage can be detrimental to offspring growth (Morganti et al., 2017), warm, wet conditions promote insect abundance (Tuero et al., 2018) and can increase nestling growth if precipitation occurs prior to hatch (Pipoly et al., 2013). Therefore, higher temperatures combined with precipitation may reflect greater food availability during peak nestling growth.

Importance of the Maternal and Developmental Environment

Environmental conditions experienced by the female prior-to or during clutch initiation have strong potential to impact offspring development and life-time fitness (Mousseau and Fox, 1998; Moore et al., 2019). Counterintuitively, colder temperatures during clutch initiation were associated with larger, heavier offspring for horned lark. While we lack the data to address maternal effects in this study, it is worth noting that this association could be adaptive if larger offspring are more robust to suboptimal conditions and if the maternal environment predicts the nestling development environment (Marshall and Uller, 2007; Weber et al., 2018). In the context of alpine birds, our results highlight that conditions experienced during clutch initiation may be an important component of offspring development and reproductive success. Research evaluating the propensity for adaptive maternal effects in alpine species would improve our understanding of how birds cope with stochastic environments.

In this study, we focused predominantly on the influence of weather conditions on offspring size and mass at 7-days post-hatch with the expectation that disrupted growth will have negative fitness consequences. Fledglings with smaller wings or tarsi are less mobile, impacting predator evasion (Martin et al., 2018). Smaller fledglings may exhibit delayed foraging independence and potentially are less likely to endure challenging weather conditions beyond the protection of the nest (Sullivan, 1989; Nord and Nilsson, 2016). Importantly, poor environmental conditions may simply delay fledging, such that nestlings leave the nest at a similar size and mass (i.e., catch-up growth; Aldredge, 2016). However, delayed fledging increases nest exposure and thus the probability of nest predation (Remes and Martin, 2002). Beyond these short-term consequences, poor developmental conditions have the potential to influence future thermal tolerance, longevity and life-time reproductive success (Lindström, 1999; Monaghan, 2008; Andreasson et al., 2018; Nord and Giroud, 2020). Longitudinal studies on individuals that evaluate these latent effects are rare, particularly in free-living populations, but are necessary to fully understand the fitness consequences of weather conditions at different stages of offspring development.

CONCLUSION

Extreme weather events are becoming increasingly common, particularly in already stochastic habitats like the alpine and arctic (IPCC, 2018). Identifying critical stages where alpine songbird reproduction is most vulnerable to inclement weather is fundamental to predicting future reproductive success under a changing climate. Horned larks were resilient to colder average temperatures but were vulnerable to prolonged periods of extreme cold and multi-day storms. Dark-eyed junco and savannah sparrow appeared less resilient to temperature challenges but were robust to storm events. Different response thresholds and susceptibilities likely reflect differences in life-history traits such as nest cover, body mass, and breeding phenology. For example, savannah sparrows may evade environmental constraints by nesting later in the season when conditions are more benign, but at the expense of a shorter breeding season. We provide evidence for stage-specific impacts of inclement weather on offspring development which advances our understanding of early-life resilience to stochastic environments. We also highlight that key life-history traits may correlate with differences among alpine species in their vulnerability to extreme weather events, such that their capacity to cope with an increasingly variable environment may be predictable.

DATA AVAILABILITY STATEMENT

The data and code are available from the Figshare data repository. Data: doi: 10.6084/m9.figshare.13070276. R code: doi: 10.6084/m9.figshare.13070267.

ETHICS STATEMENT

All procedures and protocols for this study were approved by the University of British Columbia's Animal Care Committee (A03-0095, A13-0073, and A15-0027) and are in accordance with the Canadian Council on Animal Care's national guidelines. All data were also collected under a Scientific Permit for Capture and Banding of Migratory Birds from Environment and Climate Change Canada (10365 BO, 10365 DS, and 10761 J).

AUTHOR CONTRIBUTIONS

DZ, KM, and AD conceived the ideas. DZ, JG, and KM collected the data. DZ and AD analyzed the data and led writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.570034/full#supplementary-material

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The Large Communal Nests of Sociable Weavers Provide Year-Round Insulated Refuge for Weavers and Pygmy Falcons

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The primary role of nests as structural support for eggs, nestlings, and incubating parents is well established, but our understanding of their secondary roles and their adaptive features is still limited. Nests can serve a particularly important role in protecting or buffering birds from weather. In hot, arid environments, maximum daily temperatures can exceed a species' upper critical temperature threshold and during the non-breeding season temperatures may also drop below freezing. Nest structures that help buffer against extreme temperatures may play a crucial role in managing the costs of thermoregulation, especially those nests that are used and maintained year-round. We use extensive year-round data to investigate the thermal benefits of massive colonial structures built by sociable weavers in the arid savannahs of the Kalahari, South Africa. These colonies consist of multiple nesting chambers and are used as roosts when birds are not breeding. We explored whether these structures provide thermal buffering throughout the year and how individual chamber placement within the colony and features of the chambers influenced their thermal buffering capacity. We also investigated whether nest chambers occupied and modified by an obligate nest parasite, the African pygmy falcon provided additional thermal buffering. Our results show that sociable weaver colonies provide thermal benefits throughout the year, buffering both hot and cold ambient extremes. Chambers with longer entrance tunnels provided better insulation than chambers with shorter entrance tunnels, and chambers located toward the center of a colony provided greater insulation than chambers at the edge. Chambers occupied by falcons did not display additional thermal benefits, which may be due to falcons choosing chambers with shorter entrance tunnels. Because falcons are larger than weavers, they may find it harder to enter chambers with longer entrance tunnels, and/or because weavers cease maintenance of those chambers. In conclusion, the communal nests of sociable weaver provide thermal benefits to weavers and heterospecifics alike, creating a more optimal environment for breeding, roosting and reducing thermal stress. In a landscape that is becoming increasingly harsh under climate change, the importance of these structures to the local animal communities may also increase.

Keywords: ecosystem engineers, community ecology, positive interactions, thermal refuge, environmental adjustment, shelter, Harsh climate, Environmental adaptations

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INTRODUCTION

All birds are oviparous and require nesting sites to lay their eggs (Mainwaring, 2015). The primary role of nests as structural support for eggs, nestlings, and incubating parents is well established, but our understanding of their secondary roles and their adaptive features is still limited (Heenan and Seymour, 2011; Reynolds and Deeming, 2015). However, secondary roles have been identified and include extending phenotypic signals, reducing parasite loads, reducing predation via crypsis, and moderating the micro-environment within the nests (Heenan, 2013; Mainwaring et al., 2014). These roles demonstrate that nests are multifunctional structures and are far more sophisticated than originally thought (Heenan, 2013; Mainwaring et al., 2014). Yet, studies exploring secondary roles are far less frequent than those investigating other nesting behaviors, that include incubation, brood provisioning, and nest construction (Reynolds and Deeming, 2015). This is surprising, especially when considering the great variation of nests across avian taxa, that include simple scrapes on the ground, cup nests in vegetation, nests in burrows below ground and large communal structures (Maclean, 1973a; Mainwaring et al., 2015).

The diversity of nest types suggests that functional traits of the structure may also differ between species and on the environmental conditions the species encounter. Nevertheless, our understanding of the functional properties of bird nests is still in its infancy, with the majority of studies being carried out using nest-boxes to investigate cavity nesting species (Deeming and Mainwaring, 2015). Many of these studies focus on the nests' ability to prevent eggs from cooling too quickly (Heenan, 2013; Mainwaring et al., 2014). However, in tropic, sub-tropic and desert climates, there may also be a need to prevent eggs from overheating, yet this question has received little attention (Walsberg and Voss-Roberts, 1983; Mainwaring, 2015). The frequency and duration of hot-weather events are predicted to increase in arid environments as the effects of climate change advance (Meehl and Tebaldi, 2004; Akoon et al., 2011). This has been predicted to have negative effects on avian communities (Conradie et al., 2019), that can range from increasing temperatures reducing foraging efficiency to the increased number of heat waves causing catastrophic mortality events (McKechnie and Wolf, 2010; Cunningham et al., 2015). As a result, our line of research will prove valuable for strengthening our understanding of how birds may cope with climate change.

Birds living in hot arid environments frequently face harsh climatic conditions, with temperatures repeatedly exceeding upper critical thresholds of many species (Smith et al., 2017). For example, six out of the seven desert song birds tested by Smith et al. (2017) demonstrated temperature upper thresholds that sat within a relatively narrow range (36.2–39.7°C), while the largest species tested (70 *g*) had a considerable higher threshold (42.6°C). Species may adopt behavioral or physiological adaptations that help buffer against these extreme temperatures, including moving to the shade to reduce their heat load (Tieleman et al., 2003; Cunningham et al., 2015). However, behavioral responses may be constrained if birds are restricted to a nest for large portions of the day whilst breeding. Furthermore, eggs, and nestlings may also be susceptible to thermal damage (Walsberg and Voss-Roberts, 1983). Most species maintain eggs at temperatures between 32–35°C, independent of environment or body size (Webb, 1987; Williams, 1996) but temperatures start to become lethal at about 42°C, with embryos dying quickly if they reach 44°C (Webb, 1987; Williams, 1996). As a result, parents must try to prevent their eggs from overheating by regulating the microclimate within the nest (Tieleman et al., 2008). This come with costs because birds in arid environments often experience considerable heat stress during incubation and will subsequently suffer increased water loss (Tieleman et al., 2008). Furthermore, high temperatures can slow nestling growth and increase the risk of nest failure (Cunningham et al., 2013; Rodríguez and Barba, 2016). As a result, thermal stress can be a critical factor influencing reproductive success (Walsberg and Voss-Roberts, 1983).

Temperatures during winter in arid environments can also drop below the optimal incubation temperature, and occasionally fall below freezing (Schwimmer and Haim, 2009). If birds are breeding at this time of the year, low temperatures can lead to longer incubation periods, and therefore increased risk of predation (DuRant et al., 2013). Incubating eggs below optimal temperatures can lead to nestlings with lower body mass (Ardia et al., 2010). If unattended, egg temperatures can drop rapidly (Haftorn, 1988; Weathers and Sullivan, 1989), and if they fall to 25–27°C or below for extended periods, then embryonic development stops, although short intervals of cooling are not always harmful (Webb, 1987; Williams, 1996). Furthermore, incubation is energetically costly for adults, often as expensive as chick rearing, and these costs increase at lower temperatures (Nord and Williams, 2015). For example, at experimentally lowered nest temperatures in tree swallows (*Tachycineta bicolor*), adults were unable to maintain optimal incubation temperatures and spent more time away from the nest (Ardia et al., 2010). Conversely, at experimentally heated nests, the cost of incubation for tree swallows was reduced and adults increased incubation nest attentiveness (Ardia et al., 2009). It is therefore important for incubating parents to provide a nest that can moderate temperature stress in environments where extremes in temperatures are possible (Medina, 2019). If the breeding season encompasses both hot and/or cold extremes then a nest that buffers against these will facilitate reproductive success.

Nest location, architecture, and the materials used during construction have all been shown to be important factors for buffering external ambient temperatures (Mainwaring et al., 2014). Shaded sites can reduce heat stress during the hottest times of the day or year (Orr, 1970; Tieleman et al., 2008). Enclosed nests provide protection against direct sunlight or prevailing winds (Sidis et al., 1994), with the "roof" of the nest providing shade for the eggs or chicks, during periods of high temperatures, while retaining heat during cold periods (Ricklefs and Hainsworth, 1969; Töpfer and Gedeon, 2012; Martin et al., 2017). Within species studies have demonstrated that nests built in colder climates have better heat retaining characteristics (Rohwer and Law, 2010; Crossman et al., 2011), at least partly due to the materials used to build nests (Kern and van Ripper, 1984; Briskie, 1995; Rohwer and Law, 2010). Nests in environments with frequent strong winds are built with thicker nest-walls to minimize convective heat loss (Schaefer, 1976). Mainwaring and Hartley (2008) found that as the breeding season progressed and temperature increased, the mass of the lining materials declined. Nests in wet environments lacked liners and were more porous, absorbing little water and drying rapidly (Kern and van Ripper, 1984). These studies demonstrate that selective pressures of the local climate and weather may drive much some of the variation observed between nests, and also that nests are adapted to the conditions encountered.

Some species use their nests year-round for reasons other than breeding (Forshaw, 2010). Using nest structures for roosting should provide benefits to individuals throughout the year, including the maintenance of homeothermy. This will be especially important to small species in arid environments, where the costs of endothermy are particularly pronounced (McKechnie and Lovegrove, 2002; McKechnie and Mzilikazi, 2011). When temperatures are low, birds can reduce energy demands while roosting through physiological processes including facultative heterothermic responses such as torpor, or through behaviors such as communal roosting and the use of sheltered roost sites (Lyman, 2013). When temperatures are high, birds can use the structure as a refuge, returning during hot periods to avoid direct sunlight (Maclean, 1973a). Year-round nests can also provide a permanent shelter from storms and strong winds. Furthermore, vegetation in arid environments respond strongly to rainfall and many species rely on these resources to trigger the onset of breeding (Dean et al., 2009), however, often rainfall in these areas is highly unpredictable and variable. Maintaining a year-round or permanent nesting structure should allow these species to respond quickly and appropriately to rain events. Consequently, selective pressures may differ considerably for these species and their nest/roost structures would need to deal with a range of daily and seasonal weather conditions.

Sociable weavers (*Philetairus socius;* henceforth weavers), small passerine birds (approx. 27 *g*), endemic to the semi-arid and arid Kalahari in the western parts of southern Africa, build massive colonial nest structures (Maclean, 1973a; Mendelsohn and Anderson, 1997). These large colonies are built using *Stipagrostis* grasses, and maintenance by weavers means these structures can exist for decades and host many generations of weaver (Collias and Collias, 1964). Each colony can contain between two and 250 chambers and hundreds of weaver individuals (Maclean, 1973a). Each nest chamber is accessed through its own entrance tunnel situated on the underside of the colony (**Figure 1**). Nest chambers are located at different depths (<25 cm) within the colony and therefore entrance tunnels vary in length (Maclean, 1973a). Internal nest temperatures are cooler than external temperatures in summer and warmer than external temperatures in winter (Batholomew et al., 1975; White et al.,

FIGURE 1 | The underside of a sociable weaver colony. These structures can contain many nesting chambers that are entered through the underside of the colony **(a)**. Those occupied by pygmy falcons are conspicuous due to the chalk-like fecal mat pasted around the entrance **(b)**.

1975; van Dijk et al., 2013; Leighton and Echeverri, 2014). It has also been demonstrated that chambers toward the center provide better thermal buffering against external temperatures than those on the edge (van Dijk et al., 2013; Leighton and Echeverri, 2014). This influences the weaver social dynamics, as dominant individuals occupy central chambers with greater insulation (van Dijk et al., 2013). Furthermore, when weavers are not breeding and external temperatures are low, multiple individuals (up to 8) will roost in a single chamber, this further increases the nest temperature reducing the effects of cold ambient temperatures (Paquet et al., 2016).

Sociable weaver colonies host other species, both avian and non-avian (Maclean, 1973b). Several bird species roost in the weaver chambers, while others also use the chambers for their own reproduction (Maclean, 1970, 1973b; Bolopo et al., 2019). Therefore, the thermal properties of chambers should be important, especially for those species that use the chambers for breeding. An obligate associate of weaver colonies is the pygmy falcon (*Polihierax semitorquatus*; henceforth "falcons"). Falcons are Africa's smallest diurnal raptor (approx. 60 *g*), and in southern Africa they breed and roost exclusively within weaver colonies causing their distribution within this region to overlap with weavers (Maclean, 1970). Both weavers and falcons use the colonies year-round, creating a nesting association with costs and benefits to both species (Maclean, 1970). Falcons prey on weavers' adults and chicks (Maclean, 1970; Covas et al., 2004; Spiby, 2014), and weavers alarm and often disperse when falcons are present (Lowney et al., 2020). Therefore, falcons can likely choose a chamber in the weaver colonies that are optimal for their requirements. However, chamber selection by falcons and other heterospecifics has not yet been explored. Multiple falcons may use the same chamber, with up to three individuals huddling together during winter (Lund et al., 2020), and family groups may use multiple chambers within a given colony (Bolopo et al., 2019). Interestingly, falcons defecate at their chosen chamber entrances leaving a conspicuous thick white fecal mat, though the reasons behind this remain unknown (**Figure 1**; Krochuk et al., 2018). Whether these fecal mats impact internal conditions within the chamber is unclear. The whiteness of the fecal mats at chamber entrances may reflect heat or the extra layer may provide further insulation (Mayer et al., 2009). Alternatively, the insulation qualities of the chamber may be diminished when compared to adjacent weaver chambers, but these possibilities remain unexplored.

Here we investigate the thermal properties of chambers in weaver colonies across a calendar year. Previous studies offered a first insight into the thermal properties of these colonial nests but have been limited to short sampling periods (from a few days up to 2 months), low sample sizes, or night-time measurements only. Here, we compiled the most extensive record of year-round day and night temperatures of nest chambers in weaver colonies to investigate (i) how chambers located in different parts of the nest mass (center to periphery) differ in insulation properties, and (ii) the yearly temporal dynamics of the chamber buffering relative to ambient temperatures. Furthermore, we explored the possible thermal properties of the chamber modifications made by the falcons depositing their feces at the entrance of the chamber. We hypothesized that the thick chalk-like fecal mat around the entrance of the chamber might provide extra amelioration against cold and hot temperature peaks. We also explore the chamber selection by falcons.

MATERIALS AND METHODS

Study Site

Work was conducted at Tswalu Kalahari, a reserve in the Northern Cape Province, South Africa (27°13'30?S, 22°28'40?E). Tswalu Kalahari has a hot and arid climate with mean annual temperatures of 16.8 to 18.2°C that can exceed 40°C in summer and drop below 0°C during winter. For January and July, the mean daily maximum temperatures are 35.6°C and 21.7°C, and the mean minimum temperature is 19°C and 0.6°C, respectively. On average frost occurs 27–33 days per year (van Rooyen and van Rooyen, 2017). In the period of this study we recorded 50 days where temperatures exceeded 40°C and 36 days when temperatures dropped below 5°C. Our study area consisted of 130 km^2 within the 960 km^2 reserve and contained over 250 weaver colonies, mostly in the two dominant tree species: camelthorn (*Vachellia erioloba*) and Shephard's tree (*Boscia albitrunca*). Weaver colonies at Tswalu Kalahari vary dramatically in size, and their height from the ground, in our study site, weaver nests contained an average of 50 chambers (±43 SD, range 2–244) and were on average 2.45 m from the ground (±1.07 SD, range 1–9 m).

Survey Methods

To monitor the thermal properties of weaver colonies we used Fourtec Microlite temperature loggers to record internal and ambient temperatures once every 5 min. Internal loggers were placed within the cup of nest chambers within a focal colony. Prior to placement, we inspected suitable chambers for logger insertion (see below), using a Rolson 60515 Two LED Telescopic Inspection Mirror. If eggs or chicks were observed, we would place the logger in an adjacent chamber. After placing loggers, we sealed off the chambers using chicken wire, allowing air to flow as normal and simultaneously prevent birds from entering the monitored chambers.

Sociable Weaver Chambers

We collected data on temperature within weaver chambers between 24 December 2015 and 6 January 2017. We used the R statistical package to randomly select 48 colonies to survey. For each colony sampled, we counted the number of chambers, which serve as a good proxy of nest size area (Leighton and Echeverri, 2014). In total each colony was surveyed for approximately 14 days. Initially we planned to survey each colony twice, giving 7 days of sampling each time. However, this was not always possible, therefore, some colonies were only surveyed once, and on these occasions, loggers were placed for approximately 14 consecutive days. Two colonies were sampled concurrently at any given time. After a colony had been surveyed, loggers were removed, data were downloaded and loggers were then placed in a different colony on that same day when possible. If this was not possible, then loggers were placed the following day. This meant that we increased the likelihood of acquiring max and minimum recording from every-day throughout the calendar year. As most colonies were visited twice, we usually surveyed those in opposite seasons (summer and winter, autumn and spring).

We used four loggers to record temperatures at each colony; three internally in chambers and one externally placed. Each logger was placed in a nest chamber in three different positions within a colony. The first was placed in a chamber closest to the edge of the colony, while a second was placed in a central chamber that was mid-way between the colony edges (equal distances to two edges). The third logger was placed in a chamber mid-way between the edge and center chambers. To record the ambient temperature the fourth logger was attached to the underside of a branch on the tree containing the surveyed colony, this logger was placed so that it did not receive direct sunlight. In order to understand how the location of a chamber within the nest affects its insulation properties, we recorded the depth of the chamber by measuring the length of the entrance tunnel, and the distance from the nearest edge of the colony, this was done for chambers that received temperature loggers only.

To determine the thermal properties of different weaver chambers, we extracted the highest and lowest temperature readings from each logger for each day of the survey. Additionally, we extracted the two recordings taken before and after each maximum and minimum recording (five readings in total, i.e., a 25 min period). This was to allow for a greater representation of the colony's thermal properties.

Pygmy Falcon Chambers

To determine whether falcon fecal mats at chamber entrances effect the thermal properties of weaver chambers we placed two temperature loggers in colonies hosting falcons. The first logger was placed inside an active or recently active falcon chamber. Recently used falcon chambers are characterized by the presence of white, rather than pink, fecal mats (Maclean, 1970; Krochuk et al., 2018). The second logger was placed in a chamber immediately adjacent to the falcon chamber. Data were collected during the Austral autumn (17 April – 1 May) and winter (26 June – 12 July) of 2017 and the summer (December) of 2018. Loggers took measurements every 5 min for between 6 and 8 days. We surveyed 13 colonies, five in winter, and seven in summer. Data were extracted as detailed above. Measurements regarding the size of each colony, the chambers depth and distance from the edge of the colony were also taken.

To investigate pygmy falcon chamber location selection within colonies we used data of the falcon chambers receiving temperature loggers, here we measured the chamber depth (length of entrance tunnel), and distance from the nearest outside edge as well as counting the number of colony chambers (colony size). We added falcon chamber location data from ten additional different colonies that hosted falcons, where the same chambers measurements were taken (loggers were not deployed).

Statistical Analyses

We analyzed all data using the R statistical package 3.6.3 (R Core Team, 2020). To compare temperatures between the different logger locations (external, edge chamber, intermediate chamber, and center chamber), we carried out linear mixed models (LMMs) using the lme4 package (Bates et al., 2015). Temperature was used as the response variable for all analyses, using "day" as the sampling unit; summarizing data so that each of the response variables was calculated per logger location, per day. We compared maximum and minimum temperatures for each of the logger locations. These were obtained by calculating the mean maximum and minimum temperatures for each day, from the five readings extracted. Residual distributions of the models were inspected to assess model fit. For analyses where interactions were fitted, we explored interactions where p values < 0.05 using *post hoc* tests. Interactions with $p > 0.05$ were subsequently removed from the models. We used the emmeans and emtrends functions from the emmeans package (Lenth, 2018) to undertake *post hoc* analyses to check for differences between factor levels. For each response variable, the full model terms and structure, and the error distribution used are detailed in **Appendix Table A1**.

To compare if thermal properties of weaver colonies differed across seasons, we initially tested for differences between the three internal chamber location temperatures and the ambient temperature. The logger location (external, edge chamber, intermediate chamber, and center chamber), the size of the colony (the number of chambers), and the season (spring, summer, autumn, and winter) were used as explanatory variables. Seasons were categorized as the temperature readings taken between 1 September – 30 November as spring, 1 December – 28 February as summer, 1 March – 31 May as autumn, and 1 June – 31 August as winter. To determine if the logger location differently influenced the temperature during different seasons, we fitted interactions between logger location and season. Each colony and chamber were given a unique ID, and these were both used as random effects, with chamber ID being nested within colony ID. As two colonies were sampled at a given time, date was also used as a random effect.

Secondly, we investigated if chamber properties may explain temperature variation of weaver chambers (response variable). As explanatory variables we entered the ambient temperature, the chamber location, chamber depth, and colony size. To determine if the chamber characteristics differently influence the temperature during different seasons, we fitted interactions between the external temperature and chamber depth, the external temperature and colony size, and the external temperature and location.

To compare the thermal properties of falcon chambers with adjacent weaver chambers, we focused on the seasons with the extreme temperatures, therefore maximum temperatures collected in summer and minimum temperatures collected in winter were fitted as response variables. The logger location (falcon chamber or adjacent weaver chamber), colony size, colony depth, and the distance from the edge of the colony were used as explanatory variables. Each colony was given a unique ID that was used as a random factor. However, due to the small number of falcon chambers sampled, we used paired t-tests to determine differences between the independent chamber characteristics. No differences were observed between chamber depth, and the distance from the edge, therefore these variables were omitted from all LMMs. Furthermore, colony size shared identical variation with Colony ID, therefore colony size was also omitted from our analyses.

RESULTS

Sociable Weaver Chambers

We collected temperature data for 703 days (mean days per tree = 14.9 ± 0.6 SE) from the 48 colonies. The maximum ambient and internal temperatures were 45.0°C (mean 31.1°C ± SE 0.3), and 44.0°C (28.0°C ± 0.15), respectively (**Table 1**). The maximum temperatures for chambers located at the edge of the colony were 44.0°C (28.4°C ± 0.3), while intermediate and centrally located chambers were 41.8°C (28.0°C ± 0.7) and 43.0°C (27.5°C ± 0.3), respectively (**Table 1**). The minimum ambient and internal temperatures were −3.1°C (16.7°C ± 0.3), and −2.1°C (19.6°C ± 0.2), respectively. The minimum temperatures for chambers located at the edge of the colony were −2.1°C (18.9°C ± 0.3), while intermediate and centrally located chambers were −0.4°C (20.0°C ± 0.3) and 0.4°C (19.8°C ± 0.3), respectively (**Table 1**).

TABLE 1 | Seasonal temperature readings including the minimum, maximum, mean, and standard error for each logger placement for maximum and minimum comparisons.

Type	Season	Placement	Range		Mean	SE
Maximum	Summer	Center	19.1	43.0	32.8	0.32
		Intermediate	22.7	41.8	33.4	0.29
		Edge	21.9	44.0	34.5	0.31
		External	20.9	45.0	37.3	0.29
	Autumn	Center	15.7	36.4	25.1	0.36
		Intermediate	16.7	39.4	25.8	0.39
		Edge	15.5	38.5	26.2	0.41
		External	14.3	41.0	29.0	0.42
	Winter	Center	11.9	30.2	21.1	0.32
		Intermediate	11.9	29.5	20.7	0.34
		Edge	12.6	30.1	21.0	0.37
		External	9.3	33.6	23.2	0.36
	Spring	Center	16.8	39.1	29.2	0.36
		Intermediate	17.4	40.1	29.4	0.38
		Edge	18.6	40.3	30.0	0.38
		External	18.2	43.7	33.1	0.42
Minimum	Autumn	Center	9.1	28.5	19.1	0.37
		Intermediate	9.0	27.7	19.3	0.35
		Edge	9.5	28.5	18.5	0.33
		External	6.4	25.6	16.0	0.32
	Spring	Center	8.5	31.6	20.4	0.39
		Intermediate	7.2	30.8	20.3	0.40
		Edge	6.3	29.5	20.1	0.38
		External	4.5	27.7	17.8	0.36
	Summer	Center	15.8	33.4	25.7	0.24
		Intermediate	16.7	34.0	25.9	0.23
		Edge	16.8	31.0	25.0	0.21
		External	16.1	30.0	23.1	0.19
	Winter	Center	−0.4	21.5	11.9	0.38
		Intermediate	−0.4	21.5	11.6	0.43
		Edge	−2.1	21.7	10.4	0.41
		External	−3.1	18.9	8.0	0.40

Ambient vs Internal Temperatures

Logger location and season explained significant amounts of variation of both maximum and minimum temperatures recorded (**Appendix Table A1**). *Post hoc* analyses revealed that, year-round, maximum temperatures inside colony chambers were all significantly cooler than the maximum ambient temperature, and that the differences between internal and external temperatures did not vary between seasons. Chambers on the edge of the colony were on average 2.8°C cooler (±SE 0.3, t = -13.59, and $p < 0.001$) than ambient temperatures. Whereas, central and intermediate chambers were 3.7°C (±SE 0.3, t = -18.22, and $p < 0.001$), and 3.3°C cooler (±SE 0.3, t = -15.89, and $p < 0.001$) than ambient temperatures, respectively. Furthermore, central chambers were on average 1.1°C cooler (±SE 0.2, t = 4.79, and $p < 0.001$) than chambers on the edge of the colony (**Figure 2**). Year-round minimum temperatures were all significantly warmer inside colony chambers compared to the external ambient temperature. Chambers on the edge of the colony were on average 2.3°C warmer (±SE 0.2) than ambient temperatures, whereas central and intermediate chambers were 3.1°C (±SE 0.2) and 3.2°C warmer (±SE 0.2) than ambient temperatures, respectively. Central and intermediate chambers were also on average 0.8°C (±SE 0.2, t = 4.446, and $p < 0.001$) and 0.9°C (±SE 0.2, t = 5.013, and $p < 0.001$) warmer than edge chambers (**Figure 2**). Season also explained significant variation ($\chi^2 = 472.6$, $p < 0.001$), with temperatures being warmer during summer and colder in winter. The interactions between logger location and season did not explain the variation and was removed from final models (**Appendix Table A1**).

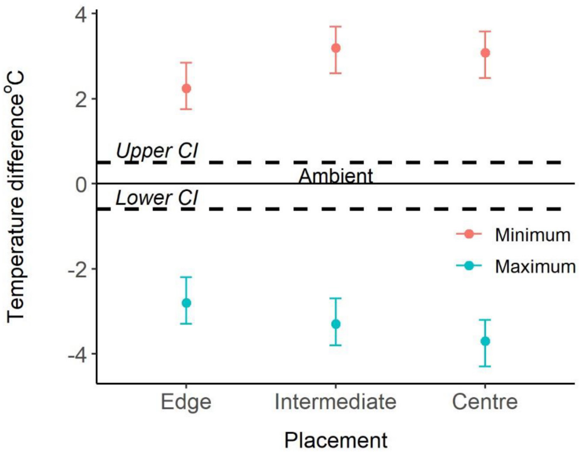

FIGURE 2 | Comparison of ambient and internal temperatures. 0°C and the solid line represent the ambient temperature, the dotted lines represent the confidence intervals, and the points represent the difference to ambient temperatures (mean ± 95% CI).

Comparison of Colony Chambers

We collected data on the characteristics of 48 colonies and 332 nesting chambers. Colony size averaged 42 chambers (±SE 2.49, range 10–102). Edge, intermediate and central chambers were 14.0 cm ± 1.0 (mean ± SE), 46.4 cm (±2.0), and 70.5 cm (±2.8) from the periphery of the colony, respectively. While chamber depth was 16.6 (±0.4), 18.6 cm (±0.4), and 19.2 cm (±0.4), respectively. Pearson's tests did not reveal any correlations between colony size and the chamber distance from the edge ($|r| = 0.05$), colony size and the depth of the chamber ($|r| = 0.11$), or between the chamber distance from the edge and the chamber depth ($|r| = 0.16$).

When we explored how the different chamber characteristics influenced temperatures within colonies, we discovered that the interactions between ambient temperatures and chamber location, and ambient temperature and chamber depth explained significant amounts of variation for both maximum and minimum temperature (**Appendix Table A1**). Moreover, the interaction between ambient temperature and colony size also explained significant variation between minimum temperatures (**Appendix Table A1**). *Post hoc* comparisons between chamber locations revealed that central and intermediate chambers provide stronger insulation than edge chambers for both maximum (central $t = -3.01$, $p < 0.01$; intermediate $t = -2.53$, $p < 0.05$) and minimum temperatures (central $t = -2.806$, $p < 0.05$; intermediate $t = -2.42$, $p < 0.05$). These chambers were cooler against high, and warmer against low ambient temperatures.

At the highest maximum ambient temperature (45.0°C), chambers on the edge of the colony were predicted by our models to be 7.5°C (±0.3) cooler, while intermediate and central chambers were 8.5°C (±0.4) and 9.0°C (±0.4) cooler, respectively (**Figure 3**). When maximum temperatures were at their lowest (9.3°C), internal chambers were all warmer. Chambers on the edge were estimated by the model to be 4.5°C (±0.5) warmer, while intermediate and central chambers were 5.1°C (±0.5) and 5°C (±0.5) warmer, respectively (**Figure 3**). When the ambient maximum temperatures were at 20°C, the maximum temperatures for all chambers was also 20°C (**Figure 3**).

At the lowest minimum temperature (−3.1°C), chambers on the edge were predicted to be 4.4°C (±0.4) warmer, while intermediate and central chambers were 6.2°C (±0.4) and 6.2°C (±0.4) warmer, respectively (**Figure 3**). When minimum temperatures were at their highest (30°C), chambers on the edge were estimated to be 0.8°C (±0.3) warmer, while intermediate and central chambers were 1.3°C (±0.3) and 1.2°C (±0.3) warmer, respectively (**Figure 3**).

Chambers with deeper entrances also provided greater insulation, being cooler during high, and warmer during low ambient temperatures (**Figure 4**). At the highest maximum ambient temperature (45.0°C), the deepest chambers (30 cm) were predicted to be 10.0°C (±0.6) cooler, while the shallowest chambers were predicted to be 6.5°C (±0.6) cooler (**Figure 4**). When maximum temperatures were at their lowest (9.3°C), deep and shallow chambers were estimated to be 5.5°C (±0.8) and 4.1°C (±0.5) warmer, respectively (**Figure 4**). At the lowest minimum temperature (−3.1°C), the deepest and shallowest chambers were predicted to be 6.9°C (±0.6) and 4.0°C (±0.7) warmer, respectively (**Figure 4**). While at the highest minimum temperatures (30°C), deeper chambers were estimated to be 0.4°C (±0.5) warmer, while shallower chambers were 1.8°C (±0.50) warmer (**Figure 4**).

Chambers inside larger colonies were cooler than those inside smaller colonies when ambient temperatures were at their coldest. However, when minimum temperatures were at their highest, chambers in larger colonies were warmer than in smaller

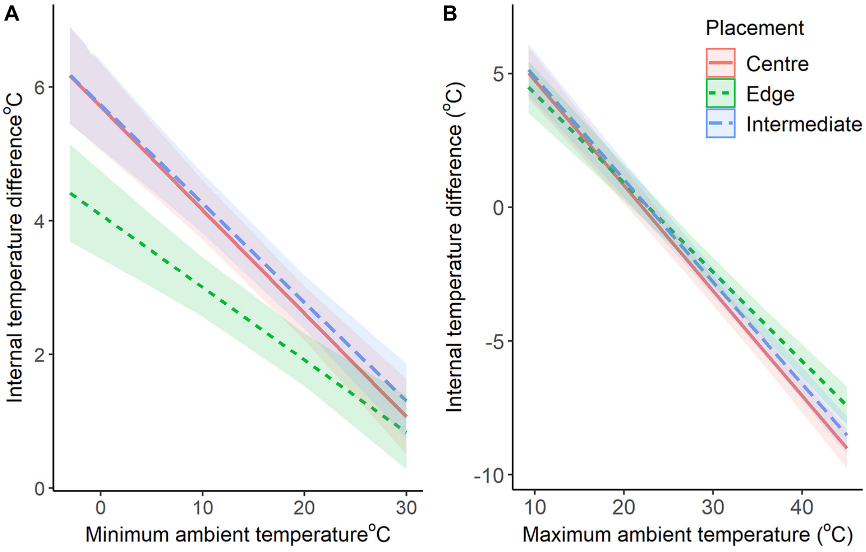

FIGURE 3 | Comparison of the buffering capabilities of nest chambers (+95% CI) against maximum **(A)** and minimum **(B)** ambient temperatures. The lines represent the difference between internal and ambient temperatures (model predicted values with 95% confidence intervals).

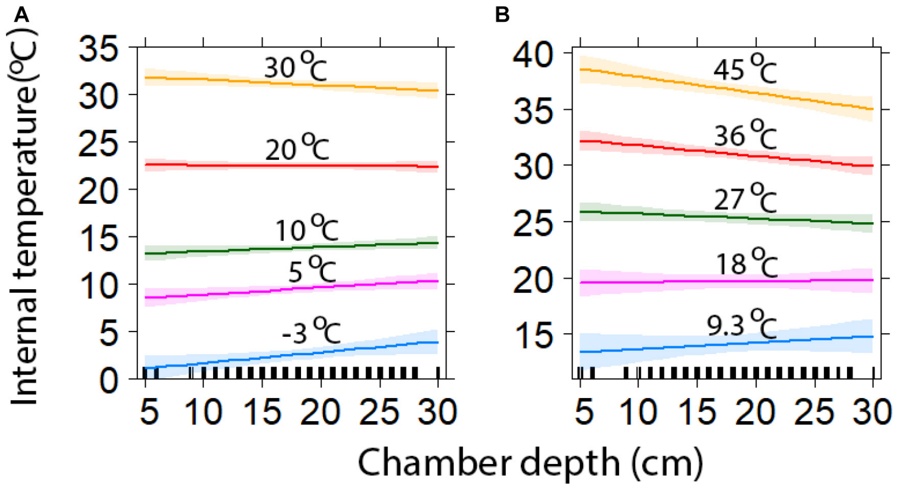

FIGURE 4 | Comparison of chamber depth insulation against minimum **(A)** and maximum temperatures (±95% CI). The lines represent a range of external temperatures for a range of minimum **(A)** and maximum **(B)** values (model predicted values with 95% confidence intervals).

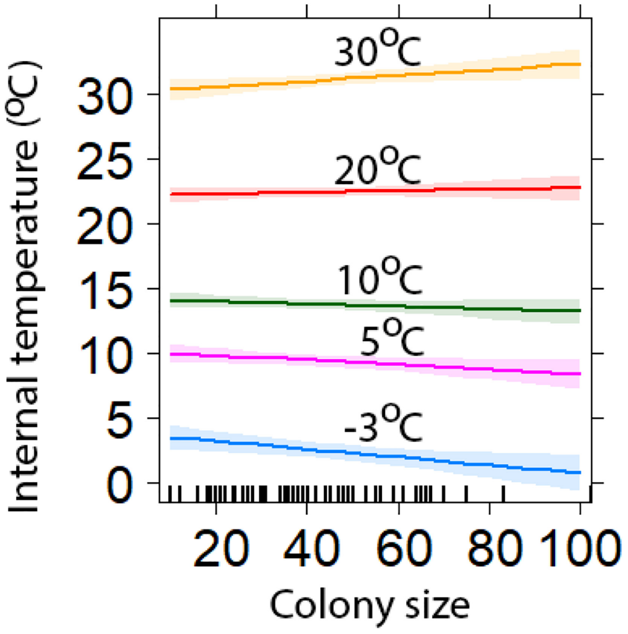

FIGURE 5 | Comparison of the insulation capabilities of different sized colonies compared with minimum temperatures (±95% CI). Colony Size is determined by the number of chambers. The lines represent a range of external temperatures for a range of minimum values (model predicted values with 95% confidence intervals).

colonies (**Figure 5**). At lowest minimum temperature (−3.1°C), the largest and smallest colonies were predicted to be 3.8°C (±0.7) and 4.0°C (±0.7) warmer, respectively (**Figure 5**). While at the highest minimum temperatures (30°C), the largest and smallest colonies were estimated to be 2.4°C (±0.6) and 0.3°C (±0.4) warmer, respectively (**Figure 5**).

Pygmy Falcon Chambers

Falcon chambers were located 40.7 cm ± 4.87 (mean ± SE) from the edge of the colony and had a mean depth of 15.0 cm (±0.1). The average maximum internal temperature in summer for falcon chambers was 36.9°C (±0.4), while for adjacent weaver chambers it was 36.3°C (±0.3). The average minimum values in winter were 13.9°C (±0.5) and 14.6°C (±0.5), respectively. Paired *t*-tests found no difference between the falcon and adjacent weaver chambers in depth and distance from the edge, likely due to non-random selection of chambers adjacent to each other. Therefore, these two explanatory variables were omitted from the analyses. Chamber type (falcon/adjacent) did not explain significant variation in chamber temperatures for maximum (χ^2 = 3.25, df = 1, and p = 0.07) and minimum (χ^2 = 2.68, df = 1, and p = 0.1) temperatures. Falcon chambers were, on average 0.6°C (±0.4) warmer and 0.7°C (±0.4) cooler in summer and winter, respectively. These differences were not statistically significant; however, the p values are likely influenced by the low sample size (**Appendix Table A2**).

DISCUSSION

Our study demonstrates that weaver nests provide a thermal buffer across all seasons, thus providing a more stable environment to roost, lay eggs, and raise chicks. Our results agree with previous studies demonstrating the importance of chamber positioning with regard to the quality of temperature buffering (van Dijk et al., 2013; Leighton and Echeverri, 2014). During summer, temperatures in chambers at the center of the colony were as much as 20% cooler than maximum ambient temperatures, and chambers at the edge were nearly 16% cooler. Furthermore, the deepest chambers were up to 24% cooler whereas shallower ones were 14% cooler. During winter, central chambers were up to three times warmer, and edge chambers twice as warm. These temperature differences likely result in substantial reductions in rest-phase energy expenditure (McKechnie and Lovegrove, 2001; Whitfield et al., 2015). In addition, as a permanent structure, weaver chambers also provide thermal buffering and shelter for heterospecifics. However, while pygmy falcons modify the chambers they occupy, by adding a fecal mat at the entrance, the thermal properties of these chambers did not differ from immediately adjacent chambers.

Year-Round Thermal Benefits for Sociable Weavers

The capacity of the colonies to buffer harsh ambient temperatures year-round is important for a species whose breeding depends on highly variable and unpredictable rainfall. The breeding season of weavers can last between 3 and 9 months (Covas, 2002). However, late rains can also mean that this breeding season is extended further and into the Austral winter, as was the case during the period of this study. Therefore, having a nesting environment that provides thermal protection throughout the year allows the weavers to respond appropriately and breed shortly after rains, even when ambient temperatures are outside viable incubation temperatures (25–42°C). Although all chambers provide refuge against hot and cold ambient temperatures, those located nearer the center and deeper into the nest mass provide greater insulation, and therefore have more stable temperatures, than those with short entrance tunnels and those located at the edge of a colony. Consequently, most weaver breeding occurs in those chambers with greater insulation (van Dijk et al., 2013).

The thermal properties of weaver colonies also provide benefits for roosting individuals, year-round (van Dijk et al., 2013; Leighton and Echeverri, 2014). This will allow birds to use chambers as an insulated refuge to conserve important water and energy supplies during times of extreme temperatures. During high temperatures, weavers can use the cooler chambers to reduce their heat load, while during cold temperatures they may be able to maintain body temperature and conserve important energy supplies (Paquet et al., 2016). However, when temperatures inside chambers are low, multiple weavers can huddle together in a single chamber to conserve body temperature, and further reduce the energetic requirements of thermoregulation (Paquet et al., 2016). Colonies not only provide thermal buffering against extreme hot and cold temperatures, they also provide refuge from strong winds and heavy rainstorms (personal observations), demonstrating that colonies are used by weavers to mitigate the harsh weather conditions of the arid environment. However, large communal nests are uncommon in arid environments, suggesting that there are negative aspects to building such structures and therefore warrants further investigation.

Our results suggest that as colony size increases, the insulation capability of the structure against low temperatures deteriorate. During cold spells, minimum temperatures inside larger colonies were lower than those recorded inside smaller colonies. However, when ambient minimum temperatures remained above 18°C the chambers inside larger colonies were warmer. Birds in warm environments have been shown to build nests that buffer against warm temperatures and lose heat quicker than those in colder environments (Rohwer and Law, 2010); we provide further support of this in our study. Moreover, birds in colder environments build nests that are better insulated against low temperatures and retain heat for longer periods (Rohwer and Law, 2010; Crossman et al., 2011). We are unsure why larger weaver colonies appear to have greater convective heat loss than smaller colonies. We speculate that in cold weather, weaver individuals may move from outer chambers to huddle in groups in more central chambers. This would cause central chambers to be warmer than those on the edge, and larger colonies may have more empty edge chambers that could increase the rate of heat loss. Additionally, it may be that our random colony selection had a disproportionate number of smaller colonies that were sampled during hot periods, however, correlation tests failed to demonstrate this. Therefore, how and why larger nests are colder than smaller nests during low temperatures remains uncertain, suggesting that selection for larger colonies is driven by factors other than insulation against local weather conditions and warrants further investigation. For example, roosting with potentially hundreds of other conspecifics, may reduce an individual's risk of predation, via a dilution effect (Eiserer, 1984; Beauchamp, 1999).

Year-Round Benefits for Pygmy Falcons

The temperatures in falcon chambers were not statistically different from adjacent weaver chambers. However, our analyses may have lacked power to detect a difference due to small sample size (summer n = 7; winter n = 5). Our analyses suggested that falcon-modified chambers were on average 0.6°C warmer in summer and 0.7°C cooler in winter than adjacent chambers, therefore falcon modification decreased the buffering potential of the chambers. Despite this, falcons still gain benefits from weaver colonies, including an insulated nest and a year-round roost that they often use to avoid storms and high temperatures during the day (personal observation). In addition, falcons are obligate users of weaver colonies; therefore, they experience all of the benefits these nests provide without the energetic cost of building or maintaining them. Falcons may have the ability to defend colonies from certain predators (Maclean, 1970), but are also will also likely suffer many of the costs that weavers do, including high nest predation and failures due to colonies collapsing (Maclean, 1973a,b). Weavers do not maintain nest chambers occupied by falcons, increasing the likelihood that these particular chambers will break off the main colony (personal observation). This lack of maintenance may also explain the insulation differences between falcon and adjacent chambers. However, falcons appear to have a preference for chambers away from the center of the colony and with shorter entrance tunnels. Although it is likely that falcons would benefit from selecting chambers with better insulation, they are larger than weavers and as a result may struggle to access chambers through longer entrance tunnels. It may also be that falcon chamber selection is also driven by other factors, such as predation risk, although this is untested. Alternatively, falcons may not need chambers with the highest buffering quality, as they may have other behaviors that help them cope with extreme temperatures. For example, Sapsford (1986) reported that the falcons can enter torpor and lower their body temperature during winter, though a recent study failed to repeat these results (Lund et al., 2020). Furthermore, falcons huddle together, with up to three individuals occupying a single chamber (Lund et al., 2020).

In summary, we use extensive year-round data to demonstrate that weaver colonies provide a refuge against hot and cold temperatures for weavers and falcons, and that this insultation varies between chamber characteristics and location. Weavers and falcons not only use these structures for breeding and roosting, but also as a refuge against the sun and inclement weather (Maclean, 1973a; Bolopo et al., 2019; Lund et al., 2020). Weaver colonies are multi-functional structures, whose thermal properties create a more optimal environment for roosting, incubating and raising chicks, making this possible throughout much of the year. This is especially important for weavers, as food required for provisioning is positively linked to the unpredictable rainfall that this area experiences, and as a result weaver breeding is strongly linked to rainfall (Covas, 2002). The falcon breeding season normally occurs during spring and into summer, and does not appear to be tied so strongly to rainfall (Maclean, 1970; Bolopo et al., 2019). This means that falcons will face high temperatures during breeding; weaver chambers provide refuge from this. Additionally, many more species use weaver colonies for breeding and/or roosting, and these would be expected to gain the similar costs and benefits as weavers and falcons. However, nothing is yet known about chamber selection by other heterospecifics and whether there is a dominance hierarchy to access favored chambers. Our results demonstrate that weaver colonies provide a thermal refuge and appear to be a nest structure evolved to provide these benefits. In a landscape that is becoming increasingly harsh under climate changes (Akoon et al., 2011), the importance of these structures to the local animal communities may also increase. Due to their sheer size, sociable weaver colonies may represent an extreme case of a nest structure that buffers the impacts of seasonal weather. However, several bird species especially in arid environments construct nests that can persist year-round, for example white-browed sparrow-weavers (*Plocepasser mahali*) and red-billed buffalo weavers (*Bubalornis niger*), and we encourage more work investigating the buffering effects of these structures.

DATA AVAILABILITY STATEMENT

The datasets underlying all analyses presented in this study have been archived at the University of Cape Town's open access institutional data repository, ZivaHub (a figshare platform), where they are publicly available at https://doi.org/10.25375/uct.13042169.v1.

ETHICS STATEMENT

The animal study was reviewed and approved by University of Cape Town, South Africa (2015/V14/RT).

AUTHOR CONTRIBUTIONS

All authors contributed to conceiving the project. AL, BK, and DB conducted the fieldwork. AL, DB, and RT contributed to analysis and interpretation of the data. AL was primarily responsible for writing the manuscript and all other authors contributed to writing, editing and, ultimately, approving of the manuscript for publication.

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APPENDIX

TABLE A1 | Linear mixed models investigating the maximum and minimum temperature variables to logger placement, season, and colony size.

Response variable	Explanatory variables	Estimate ± SE	χ2	df	*P* value
(a) Maximum temperatures	Logger placement		407.22	3	<0.001
	Season		471.05	3	<0.001
	Colony size	−0.01 ± 0.01	2.12	1	0.14
	Interaction removed				
	Logger placement * Season		16.195	9	0.06
(b) Minimum temperatures	Logger placement		383.10	3	<0.001
	Season		614.29	3	<0.001
	Colony size	−0.005 ± 0.008	0.31	1	0.58
	Interaction removed				
	Logger placement * Season		5.75	9	0.77
(c) Maximum temperatures	Logger placement		10.97	2	<0.01
	Depth	0.109 ± 0.07	6.02	1	<0.05
	Colony size	−0.001 ± 0.01	0.01	1	0.91
	External temperature	0.71 ± 0.04	1758.63	1	<0.001
	External temperature * placement		10.41	2	<0.01
	External temperature * depth	−0.006 ± 0.002	6.03	1	<0.05
	Interaction removed				
	External temperature * size	0.0003 ± 0.0006	0.42	1	0.51
(d) Minimum temperatures	Logger placement		28.89	2	<0.001
	Depth	0.097 ± 0.04	0.09	1	0.77
	Colony size	−0.06 ± 0.01	0.0005	1	0.98
	External temperature	0.87 ± 0.04	4874.33	1	<0.001
	External temperature * size	0.001 ± 0.0004	14.01	1	<0.001
	External temperature * placement		9.25	2	<0.01
	External temperature * depth	−0.005 ± 0.002	6.68	1	<0.01

Interactions with P values greater than 0.05 were removed from the final models.

TABLE A2 | Linear mixed models comparing the maximum and minimum temperatures in falcon and weaver colonies.

Response variable	Explanatory variables	Estimate ± SE	χ2	df	*P* value	*N*
(a) Maximum temperatures	Logger placement (falcon/weaver)	−0.70	3.25	1	0.07	7
(b) Minimum temperatures	Logger placement (falcon/weaver)	0.73	2.67	1	0.1	5

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Shorebird Reproductive Response to Exceptionally Early and Late Springs Varies Across Sites in Arctic Alaska

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While increases in overall temperatures are widely reported in the Arctic, large inter-annual variation in spring weather, with extreme early and late conditions, is also occurring. Using data collected from three sites in Arctic Alaska, we explored how shorebird breeding density, nest initiation, nest synchrony, nest survival, and phenological mismatch varied between two exceptionally early (2015 and 2016) and late (2017 and 2018) springs. We assessed these differences in the context of long-term data from each site and whether species exhibited conservative or opportunistic reproductive strategies. Conservative shorebirds typically display nest-site fidelity and territoriality, consistent population densities, relatively even individual spacing, and monogamous mating systems with bi-parental incubation. In contrast, opportunistic shorebirds display the opposite traits, and a polygamous mating system with uniparental incubation. In this study, we evaluated 2,239 nests from 13 shorebird species, 2015–2018, and found that shorebirds of both strategies bred earlier and in higher numbers in early, warm springs relative to historic levels (based on 3,789 nests, 2005–2014); opposite trends were observed in late springs. In early springs, nests were initiated less synchronously than in late springs. Nest survival was unrelated to spring type, but was greater in earlier laid nests overall. Invertebrate food resources emerged earlier in early springs, resulting in a greater temporal asynchrony between invertebrate emergence and chick hatching in early than late springs. However, invertebrate abundance was quite variable among sites and years regardless of spring type. Overall, our results were generally consistent with predicted relationships between spring conditions and reproductive parameters. However, we detected differences among sites that could not be explained by other ecological factors (e.g., predators or alternative prey). Differences in shorebird community composition and other subtler methodological/ecological differences among sites highlight the difficulty of understanding the complex nature of these ecological systems and the importance of evaluating questions at multiple sites across multiple years. Our study demonstrates that shorebirds exhibit a high degree of behavioral flexibility in response to variable Arctic conditions, but whether this flexibility is enough to allow them to optimally track changing environmental conditions or if evolutionary adjustments will be necessary is unknown.

Keywords: Arctic, environmental variation, nest density, nest initiation, nest survival, nest synchrony, trophic mismatch, wader

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INTRODUCTION

The timing of reproduction is a central topic in avian biology (Perrins, 1970; Drent and Daan, 1980). The general consensus is that species generally time breeding efforts to coincide with periods of high food availability (Lack, 1968). For migratory birds, the timing of such efforts relies on the successful integration of circannual and environmental cues (Gwinner, 1996). In response to recent climate warming, many migratory bird species have adjusted the timing of arrival and breeding efforts to coincide with earlier spring conditions (Crick et al., 1997; Forchhammer et al., 1998; Stenseth et al., 2002; Walther et al., 2002; Parmesan and Yohe, 2003). Other studies indicate that species that are unable to advance their arrival dates may experience negative population consequences (Møller et al., 2008; Kwon et al., 2019); arrival dates may be further constrained by migratory life history, diet, or breeding habitat (Both and Visser, 2001; Jonzén et al., 2006; Both et al., 2010). Disentangling the factors that affect the timing of avian reproductive efforts is especially complex in an era of climate warming (Miller-Rushing et al., 2010; Mortensen et al., 2016).

The ability of individuals to adjust their reproductive phenology may be especially challenging for migratory birds that breed in the Arctic. Because temperatures in the Arctic are increasing more rapidly than in other regions of the earth (Serreze and Francis, 2006; Hodgkins, 2014), environmental cues that migratory animals use to order their annual cycles may now be less reliable due to a spatial decoupling of broad-scale environmental conditions (Robinson et al., 2009; Both et al., 2010). Although long-distance migrations enable individuals to take advantage of abundant food resources, lower predation pressure, reduced competition, and lower pathogen loads found in the Arctic (Gilg and Yoccoz, 2010), Arctic-breeding birds must contend with very short breeding seasons, harsh climatic conditions, and now, rapidly changing, variable, and unpredictable environmental conditions caused by climate change (Meltofte et al., 2007a; Schmidt et al., 2019). The rapid rate of warming at northern latitudes has led to earlier, warmer, and longer summers in these regions (Richter-Menge et al., 2019). In addition, summer rainfall has increased significantly (Kattsov and Källén, 2005) and winter snowfall is predicted to increase at high latitudes (Räisänen, 2007), with as much as a 21% increase in northern Alaska by the end of the century (Littell et al., 2018). Increased snowpack may counter warming temperatures and decrease the rate of snowmelt, but it is unclear how this will alter large-scale hydrological patterns (Musselman et al., 2017). Along with a general warming pattern, both spring and summer weather has also exhibited extreme annual variation (Richter-Menge et al., 2019). As such, these new changes to annual weather conditions have the potential to greatly impact the reproductive demographics of birds in Arctic environments (Schmidt et al., 2019).

Shorebirds are one of the most diverse and abundant avian taxonomic groups of the Arctic environment, with 41 species (117 subspecies or populations) migrating to the Arctic to breed (Smith et al., 2020). Three potential demographic metrics that may be influenced by annual weather conditions are nest density, nest initiation, and nest synchrony. Shorebirds time their arrival in the Arctic after long migrations to coincide with appropriate spring environmental conditions (Meltofte et al., 2007a; Ward et al., 2016; Ely et al., 2018). Beyond the need for open habitats in which to nest, shorebirds are insectivorous, and the availability of invertebrates is critical to these species, which exploit them to sustain bodily functions, develop eggs, and for young to grow (Klaassen et al., 2001; Piersma et al., 2003; Saalfeld et al., 2019). Temperature and the timing of snowmelt affect the availability of invertebrates in Arctic ecosystems (Høye and Forchhammer, 2008; Tulp and Schekkerman, 2008; Bolduc et al., 2013; Saalfeld et al., 2019), with later snowmelt and colder temperatures equating to later activity (as terrestrial invertebrates break diapause) and emergence (adult eclosion from juvenile stages) of invertebrates due to the direct link between development and sediment temperatures (Custer and Pitelka, 1978; Butler, 1980). However, the timing of shorebird arrival in the Arctic is largely driven by environmental conditions that affect departure time from wintering sites (Rowan, 1925; Gwinner and Helm, 2003; Battley, 2006). Evidence suggests some shorebirds can delay, or even back-track, while on migration if they encounter inclement weather as they near the breeding grounds (Senner et al., 2015; Ely et al., 2018), but shorebirds are likely unable to meaningfully speed up migration if spring conditions in the Arctic are much earlier than average (Saalfeld and Lanctot, 2017). In years of severe weather and late arrival of spring, shorebirds are thought to forego breeding altogether or depart to other areas to breed (Meltofte et al., 2007a and references therein), which could alter local densities of shorebirds (Saalfeld and Lanctot, 2015, but see Robinson et al., 2014).

In years of early snowmelt, shorebirds have been shown to lay eggs shortly after arrival on the breeding grounds (Klaassen et al., 2001; Meltofte et al., 2007b), while breeding is delayed in years with later snowmelt (Smith et al., 2010; Liebezeit et al., 2014). The time between arrival and egg-laying may be determined by food availability during the pre-laying period (Meltofte et al., 2007b), as well as the availability of snow-free sites to nest (Mayfield, 1978; Smith et al., 2010). Recent studies have shown that species have advanced nest initiation dates over several decades as spring temperatures have increased (McKinnon et al., 2012; Liebezeit et al., 2014; Saalfeld and Lanctot, 2017, but see Reneerkens et al., 2016), although in most cases not sufficiently fast to keep up with earlier snowmelt. Further, nest synchrony is likely to increase if time constraints imposed by late, cold springs limit when appropriate conditions to breed are available (Nol et al., 1997; Meltofte et al., 2007b; Smith et al., 2010). Additionally, the ability to nest early may also enable species to renest should their first clutch fail, which would result in more asynchronous nesting. Thus, the breeding density and patterns of nest initiation of Arctic-breeding shorebirds are sensitive to spring conditions, but not always in predictable ways.

Spring weather conditions may also impact egg and chick survival through changes in predation rates and timing of invertebrate availability. In years with a deeper snowpack and late snowmelt, the survival of alternative prey—a term used to denote food resources, such as arvicoline rodents (lemmings and voles), that predators of shorebirds and their nests may alternatively consume—often increases, yielding higher abundances during spring and summer (Korslund and Steen, 2006; Kausrud et al., 2008). The presence of higher numbers of alternative prey may promote increased numbers of breeding shorebirds (Blomqvist et al., 2002; Robinson et al., 2014) and mitigate the risk of predation on their nests (Bêty et al., 2002; Smith et al., 2007; McKinnon et al., 2012, but see Weiser et al., 2018a). Persistent spring snow cover may also directly increase the predation of shorebird nests, as late-melting snow limits the area available for nesting, allowing predators to concentrate their search effort (Byrkjedal, 1980; Meltofte et al., 1981; Machín et al., 2019), and the growth of vegetative cover is phenologically delayed making nests more obvious (Laidlaw et al., 2020). However, late-melting snow may also lead to synchronous nesting that could dilute the risk of predation to any one nest (Smith et al., 2010). Because Arctic-breeding shorebirds are primarily income breeders (Klaassen et al., 2001; Piersma et al., 2003, but see Hobson and Jehl, 2010), changes in the timing and abundance of invertebrates may in turn affect shorebird nest attendance due to adult food limitations (Tulp and Schekkerman, 2006; Reneerkens et al., 2011). Adults leaving nests unattended or making more trips away from the nest may increase the likelihood of predation by reducing crypsis of the eggs (adults are better camouflaged than eggs themselves) or drawing attention to the nest (activity near a nest can reveal its location, Smith et al., 2007, 2012; Reneerkens et al., 2011; Bulla et al., 2016; Meyer et al., 2020). But evidence linking warm springs with increased nesting success is equivocal; Weiser et al. (2018a) found limited evidence for such a relationship, with only two of 14 species investigated across a broad geographic region of the Arctic having higher nest survival in warm springs. The availability of invertebrates also directly affects the ability of young to forage and survive, with mismatches between invertebrate availability and chick hatching predicted to be especially decoupled in early springs when shorebirds do not arrive early enough to time their breeding efforts with invertebrate availability (McKinnon et al., 2012; Machín et al., 2018; Kwon et al., 2019; Saalfeld et al., 2019).

Seasonal weather patterns are unlikely to affect reproductive responses of all shorebird species in the same way (Smith et al., 2010; Robinson et al., 2014; Taylor et al., 2018; Machín et al., 2019). One overarching ecological factor that might explain the ability of shorebirds to adapt to changing climatic conditions on Arctic breeding grounds is their reproductive strategy. Arctic-breeding shorebirds have previously been broadly grouped into two reproductive strategies termed 'conservative' and 'opportunistic' depending on a number of characteristics (Holmes, 1966, 1971; Pitelka et al., 1974). Conservative shorebirds typically display strong nest-site fidelity and territoriality, monogamous mating systems with bi-parental incubation and chick care, and are generally evenly spaced across appropriate habitats. On the other hand, opportunistic shorebirds typically display low nest-site fidelity, a polygamous mating system with uniparental incubation and chick care, and occur patchily and in variable numbers from year-to-year across appropriate habitats. Pitelka et al. (1974) hypothesized that by returning to the same breeding locations each year, conservative species would have an increased knowledge of local resources, allowing at least a moderate number of offspring to be produced annually, regardless of local conditions. In contrast, opportunistic shorebirds would theoretically have a greater opportunity for more offspring to be produced in some years or locations by forgoing site fidelity and instead selecting the most favorable annual breeding locations. Only two studies on shorebirds have evaluated whether being conservative or opportunistic affected breeding response to seasonal variation in environmental conditions (Saalfeld and Lanctot, 2015, 2017). They found that conservative species tended to have low variability in annual nest densities, and that there were some phenotypically flexible adjustments in most species to snowmelt, although opportunistic species appeared to adjust better than conservative species.

Clearly, the large number of factors that affect shorebird breeding parameters interact and their effects are difficult to disentangle, especially with the influence of regional and local climate change operating directly and indirectly in the background (Juhasz et al., 2020). In this study, we took advantage of two exceptionally early and late springs to evaluate how shorebirds were affected by weather conditions at three sites on the Arctic Coastal Plain of Alaska. Response to variable local conditions can provide insight to how shorebirds may adapt to future climatic conditions, allowing winners and losers of climate change and seasonal variability to be identified. We analyzed how nest density, nest initiation dates, nest synchrony, nest survival, and phenological mismatch differed between early and late springs (relative to long-term data collected over many years) within three shorebird communities as a function of their reproductive strategies. To better understand the influence of other confounding factors, we also summarized the occurrence of potential alternative prey (arvicoline rodents) and shorebird nest predators (avian and mammalian). Our goal was to identify life-history traits that may help shorebirds moderate the effects of environmental stochasticity.

We summarized our predictions of how spring weather conditions and other important interacting factors may affect Arctic-breeding shorebirds in **Table 1**. First, we predicted that opportunistic species would nest in higher densities during early springs and in lower densities in late springs, as low site-fidelity affords these species the opportunity to select the most favorable annual breeding locations. This prediction assumes opportunistic species have the ability to assess conditions over large geographic areas and use the timing and rate of snowmelt to make settlement decisions (Pitelka et al., 1974; Lanctot and Weatherhead, 1997; Kempenaers and Valcu, 2017). In contrast, due to their site-fidelity, we predicted that conservative species would nest at consistently similar densities to their historic levels in early springs, but in lower densities during late springs, as late springs may inhibit individuals from acquiring the necessary exogenous reserves for egg laying (Nol et al., 1997; Meltofte et al., 2007b; Smith et al., 2010). Second, we predicted earlier nest initiation dates in early springs and later initiation dates in late springs for all species. However, we predicted a greater response in these dates for opportunistic species given their greater ability to track annual spring conditions as compared to conservative species. Third, we predicted that all

TABLE 1 | Predictions of how shorebirds would respond to early and late spring conditions by opportunistic and conservative reproductive strategies and the outcomes at Utqiaġvik, Colville River, and Prudhoe Bay, 2015–2018.

Factor	Predictions for conservative species	Predictions for opportunistic species	Outcome Utqiaġvik	Outcome Colville River	Outcome Prudhoe Bay
Nest density	No change in nest densities in early springs but lower densities in late springs	Higher nest densities in early springs, lower densities in late springs	Yes	Equivocal; both conservative and opportunistic species had higher nest densities in early springs	Equivocal; opportunistic species had slightly higher nest densities in early springs
Nest initiation	Marginally earlier nest initiation dates in early springs; marginally later nest initiation dates in later springs	Earlier nest initiation dates in early springs; later nest initiation in later springs; greater response than conservative species	Yes	Equivocal; both conservative and opportunistic species had earlier nest initiation dates in early springs but at similar rates	Equivocal; both conservative and opportunistic species had earlier nest initiation dates in early springs but at similar rates
Nest synchrony	Less synchrony in early springs; greater synchrony in late springs	Less synchrony in early springs; greater synchrony in late springs; greater response than conservative species	Yes	Yes; but conservative and opportunistic species had similar nest synchrony	Equivocal; conservative species did not show consistent results between early and late springs
Nest survival	Higher survival in early springs; lower survival in late springs	Higher survival in early springs; lower survival in late springs	Yes; but variable rates across late springs for opportunistic species	No	No
Phenological mismatch	Greater mismatch in early springs	Greater mismatch in early springs; lower response than conservative species	Equivocal; only one early spring showed evidence of mismatch	Equivocal; only one early spring showed evidence of mismatch	-No data-

species would exhibit greater nest synchrony in late springs due to time constraints limiting when appropriate conditions are available. During early springs, however, we predicted reduced nest synchrony for all species, as being able to lay earlier affords individuals more time to lay both initial and replacement nests. However, as opportunistic species may be better able to respond to earlier conditions (see above), we predicted even less synchrony in opportunistic species. Fourth, we predicted lower nest survival for all species in late springs, as birds may be forced to breed in snow-free patches that are more easily searched by predators (Machín et al., 2019, notwithstanding the potential benefits of nesting synchronously) and because vegetative cover is delayed. We predicted an opposite pattern in early springs, with all species having higher nest survival. Finally, we predicted that early springs would lead to a phenological mismatch between invertebrate availability and nest hatching dates for all species, although opportunistic species might be more resilient to potential mismatches due to their greater ability to adjust to local conditions.

MATERIALS AND METHODS

We monitored seasonal weather conditions and shorebirds at three field sites in northern Alaska: Utqiaġvik (71° 17′ N, 156° 47′ W), Colville River (70° 26′ N, 150° 40′ W), and Prudhoe Bay (70° 19′ N, 148° 42′ W) from 2015 to 2018. Long-term data, dating back as far as 2005, were obtained from each site to compare to these 4 years. All three sites are located on the Arctic Coastal Plain, with the maximum distance between sites about 325 km. All sites consist of a mosaic of low, wet marsh habitats and higher, well-drained upland habitats (Kessel and Cade, 1958; Brown et al., 1980). Utqiaġvik is located at the northern most portion of Alaska (Point Barrow), and as such, has a colder, later summer on average (Taylor et al., 2018). Utqiaġvik (Taylor et al., 2018) and Prudhoe Bay (Liebezeit et al., 2009) were in areas of human development, but study plots were placed >300 m from roads and buildings to minimize any potential influence of human activity (see, e.g., Liebezeit et al., 2009). The Colville River site is located on the outer delta of the river (Hupp et al., 2017). All sites followed a common set of field protocols and data formats developed for the Arctic Shorebird Demographics Network (see brief descriptions below, Brown et al., 2014). Plot size varied by site, with six study plots at Utqiaġvik (each 600 × 600 m, 216 ha total), one large plot at the Colville River that was initially 323 ha in size (2011–2016), but reduced to 262 ha in 2017, and 12 plots at Prudhoe Bay (each 100 × 1000 m, 120 ha total).

Weather

To assess seasonal differences in weather among years (i.e., 2015–2018), we obtained daily temperature data from the nearest meteorological station (National Climate Data Center, 2020) located at Utqiaġvik (Wiley Post-Will Rogers Memorial Airport ∼10 km away from our study plots), Colville River (Colville Village located ∼10 km away), and Prudhoe Bay

(Deadhorse Airport 2–21 km away). From these data, we calculated cumulative daily temperatures in June for each year by summing average daily temperatures (average of the minimum and maximum temperature for a given day) for each day in June. Using the same technique, we also generated long-term temperature averages for the 10 years prior to the study (i.e., 2005–2014).

We determined the loss of snow at our sites in each year by estimating the percent daily snow cover on plots every 2–5 days between late May and the end of June or until 10% snow cover remained. Using these data, we averaged snow cover estimates across all survey locations at each site for each survey day and extrapolated estimates to dates between survey days to generate the percentage of snow cover for each day in June. When average snow cover was < 10% before the end of June, we assumed no snow remained 2 days after the last survey. Additionally, when snow surveys started after 1 June, we removed days in early June when data were not available. Using the same approach, we also generated long-term averages of snow cover for each day in June that had data for all years (i.e., Utqiaġvik and Prudhoe Bay: 2005–2014, Colville River: 2011–2014).

Alternative Prey and Predator Abundance

The number of arvicoline rodents (alternative prey) and avian and mammalian predators were determined at each site and year using incidental observations each day by field staff conducting other field activities. Using these counts, we estimated the number of arvicoline rodents [voles (*Microtus* sp.) and lemmings (*Dicrostonyx* sp.)], foxes [arctic (*Vulpes lagopus*) and red (*V. vulpes*)], and avian predators [Glaucous Gull (*Larus hyperboreus*), Pomarine Jaeger (*Stercorarius pomarinus*), Parasitic Jaeger (*S. parasiticus*), Long-tailed Jaeger (*S. longicaudus*), Common Raven (*Corvus corax*), Sandhill Crane (*Antigone canadensis*), Snowy Owl (*Bubo scandiacus*), Short-eared Owl (*Asio flammeus*), Golden Eagle (*Aquila chrysaetos*), Peregrine Falcon (*Falco peregrinus*), Gyrfalcon (*F. rusticolus*), Northern Harrier (*Circus hudsonius*), Ruddy Turnstone (*Arenaria interpres*), and Rough-legged Hawk (*Buteo lagopus*)] observed per person per day by dividing the total number of individuals within each category observed in June by the average number of people in the field per day and the total number of days in June that observations occurred. For comparison, we also generated long-term (i.e., Utqiaġvik: 2005–2014, Colville River: 2011–2014, Prudhoe Bay: 2010–2014) estimates of these abundances for June using the same techniques. Incidental counts of alternative prey such as these correlate strongly with exhaustive mark-recapture techniques used to estimate abundance (Fauteux et al., 2018). While this may not be true for some predators (e.g., counts of fox, Liebezeit and Zack, 2008), our goal was to broadly generalize the abundance of alternative prey and predators in our two early and two late springs relative to long-term counts. Doing so allowed us to better eliminate potentially confounding factors impacting our analysis of the inter-annual variation in shorebird responses.

Invertebrate Availability

To estimate invertebrate biomass at Utqiaġvik and Colville River (no invertebrate data were collected at Prudhoe Bay), we used 10–16 modified "Malaise" pitfall traps equally distributed among mesic and xeric tundra habitats to capture available invertebrates throughout the nesting season. These traps consisted of a 38 cm × 5 cm × 7 cm plastic container placed at ground level that captured non-flying invertebrates, and a 36 cm × 36 cm mesh screen placed perpendicular above the container to capture aerial invertebrates that hit the screen and fell into the trap (Brown et al., 2014). These traps act passively to measure both abundance and activity levels of invertebrates, and as such, have previously been used as a proxy for invertebrate availability for insectivorous birds in the Arctic (Schekkerman et al., 1998, 2003; Bolduc et al., 2013; Saalfeld et al., 2019). We typically sampled traps every 3 days between early June and late July. Individual prey items were identified to family or order and length was measured to the nearest 0.25 mm for individuals < 2 mm and to the nearest 0.5 mm for individuals > 2 mm. We calculated mass for each individual using published length-mass regression equations based on taxon (Rogers et al., 1977; Schoener, 1980; Sage, 1982; Gowing and Recher, 1984; Wrubleski and Rosenberg, 1990; Sample et al., 1993; Hódar, 1996; Ganihar, 1997; Hawkins et al., 1997; Lang et al., 1997; Sabo et al., 2002). We estimated total biomass per trap day (assuming equal biomass for all days within a sampling period) for all invertebrates except large-bodied bees and wasps within the order hymenoptera. The latter are likely too large for most shorebirds to consume (Pearce-Higgins and Yalden, 2002; Schekkerman and Boele, 2009).

Shorebird Reproduction Metrics

We located shorebird nests by conducting area searches or dragging ropes across the tundra to flush adults from nests and by following birds exhibiting behaviors indicative of nesting back to their nests (Brown et al., 2014). Search effort varied between sites. At Utqiaġvik, one rope drag was conducted toward the end of June and daily searches were conducted 6 days per week throughout June on each plot (4 h per day, Saalfeld and Lanctot, 2015). At the Colville River, 2–3 observers searched the study plot for 6–8 h each day during June. At Prudhoe Bay, study plots were searched for nests using alternating rope and single-person area searches (two each) between early and late June (Bentzen et al., 2017).

We estimated nest initiation date (date first egg laid) based on the number of eggs if nests were found during egg-laying (assuming 1 egg laid per day for all taxa, although plovers may take 1.5 days, Colwell, 2006), or by back-calculating from known hatch date using standard incubation duration. If these two methods could not be used, we employed an egg-floatation technique to estimate nest initiation (Sandercock, 1998; Liebezeit et al., 2007; Brown et al., 2014). This technique relies on the fact that eggs lose mass as the embryos inside develop, causing them to sink initially and later float in water. Nests were revisited generally every 5 days during incubation. We recorded a nest as hatched if at least one chick was observed in the nest, or if eggshell fragments indicative of hatching, or an egg tooth, were found in the nest within 4 days of the expected hatch date (Mabee, 1997; Brown et al., 2014). We recorded the hatch date as (1) the day that downy chick(s) were first found in the nest, (2) the day after eggs were observed with pipped holes in the shells, or (3) 2 days after eggs were observed with star-cracks in the shells (Brown et al., 2014). We classified nests as unsuccessful or failed if we found broken eggshells indicative of predation in the nest, if the clutch disappeared more than 4 days before the predicted hatch date, or if the eggs remained unattended by parents for ≥ 3 days. We recorded nest fate as unknown if there was unclear or conflicting evidence at the nest site (Brown et al., 2014). If fate was unknown ($n = 108$), nests were considered successful until the last day they were known to be active (a metric important for the nest survival analysis). We did not include nests found at hatch for nest survival analyses.

Statistical Analyses

Based on air temperature and snow conditions, we classified each year as having a spring that was either "early" or "late" (hereafter 'spring'). We also grouped species into either a conservative or opportunistic reproductive strategy (hereafter 'strategy') based on Saalfeld and Lanctot (2015) (**Table 2**). In the case of the Long-billed Dowitcher, which exhibits traits of both strategies, we considered it an opportunistic breeder because of its low to non-existent site fidelity and territoriality, which likely has the most effect on the reproductive predictions tested here (Saalfeld and Lanctot, 2015; Takekawa and Warnock, 2020).

We used general linear models (PROC MIXED, SAS Institute, Inc., Cary, NC, United States) with each nest treated as an independent data point to evaluate the categorical effects of site, year, spring, and strategy on nest initiation date. Here, we used an *a priori* model set consisting of all single variable models, as well as all additive and multiplicative combinations of the above variables (25 models). We used all possible model combinations in our analysis because all variables and their interactions were thought to be biologically meaningful. However, we restricted models so that year and spring did not enter the same model. We also did not include information on alternative prey, predators, and invertebrates because there was no meaningful variation (alternative prey and predators) or data was not available for all sites (invertebrates at Prudhoe Bay). Similarly, we used the same *a priori* model set (with the inclusion of nest initiation date as a continuous effect) and data structure to investigate variation in daily nest survival using Program MARK (White and Burnham, 1999; Dinsmore et al., 2002). For all multi-model comparisons, we used Akaike's Information Criterion corrected for small sample sizes (AIC_c), in which we considered the model with the lowest AIC_c value to be the best-supported, and models with a $\Delta\text{AIC}_c < 2$ to be plausible (Burnham and Anderson, 2002).

For each site, year, and reproductive strategy, we also calculated estimates for nest density (i.e., cumulative number of nests found throughout study plot(s) divided by the total area of the plot(s) in ha) and nest synchrony (i.e., standard deviation of nest initiation dates of the cumulative number of nests throughout study plot(s); Nol et al., 1997). When calculating nest densities, we restricted nests to those found in the smaller study plot at the Colville River across all years.

For comparison to the early and late springs that were the focus of this study, we also generated long-term estimates of nest density, nest initiation, nest synchrony, and nest survival for all years (i.e., Utqiaġvik and Prudhoe Bay: 2005–2014, Colville River: 2011–2014 [small plot for nest density, and large plot for other parameters]). Here, we compared values from the early and late springs to the long-term median values to determine whether an effect was present (i.e., value was above or below the median value as predicted).

TABLE 2 | Number of shorebird nests by species located at Utqiaġvik, Colville River, and Prudhoe Bay, 2015–2018.

	Utqiaġvik	Colville River[a]	Prudhoe Bay	Reproductive strategy[b]
Black-bellied Plover, *Pluvialis squatarola*	0 (0)	25 (18)	1 (3)	Cons
American Golden-Plover, *Pluvialis dominica*	40 (100)	0 (1)	4 (10)	Cons
Semipalmated Plover, *Charadrius semipalmatus*	0 (0)	0 (1)	0 (0)	Cons
Bar-tailed Godwit, *Limosa lapponica*	0 (0)	5 (1)	0 (0)	Cons
Ruddy Turnstone, *Arenaria interpres*	0 (1)	16 (26)	0 (1)	Cons
Stilt Sandpiper, *Calidris himantopus*	0 (0)	1 (0)	18 (41)	Cons
Dunlin, *Calidris alpina*	136 (336)	56 (55)	12 (24)	Cons
White-rumped Sandpiper, *Calidris fuscicollis*	0 (6)	0 (0)	0 (0)	Oppor
Buff-breasted Sandpiper, *Calidris subruficollis*	0 (15)	0 (0)	2 (6)	Oppor
Pectoral Sandpiper, *Calidris melanotos*	255 (552)	53 (18)	62 (167)	Oppor
Semipalmated Sandpiper, *Calidris pusilla*	110 (259)	417 (323)	105 (302)	Cons
Western Sandpiper, *Calidris mauri*	64 (91)	1 (0)	0 (0)	Cons
Long-billed Dowitcher, *Limnodromus scolopaceus*	65 (197)	0 (2)	15 (20)	Oppor
Red-necked Phalarope, *Phalaropus lobatus*	46 (71)	51 (62)	47 (82)	Oppor
Red Phalarope, *Phaloropus fulicarius*	544 (883)	75 (69)	13 (46)	Oppor
Total	1, 260 (2, 511)	700 (576)	279 (702)	

Number of nests from past years at each site is listed parenthetically: Utqiaġvik (2005–2014), Colville River (2011–2014), and Prudhoe Bay (2005–2014). [a]*An additional 63 nests were located outside the smaller plot boundary in 2015–2018 (83 in 2011–2014) that were used for nest initiation, nest synchrony, and nest survival analyses.* [b]*See text for definition of conservative (Cons) and opportunistic (Oppor) reproductive strategies.*

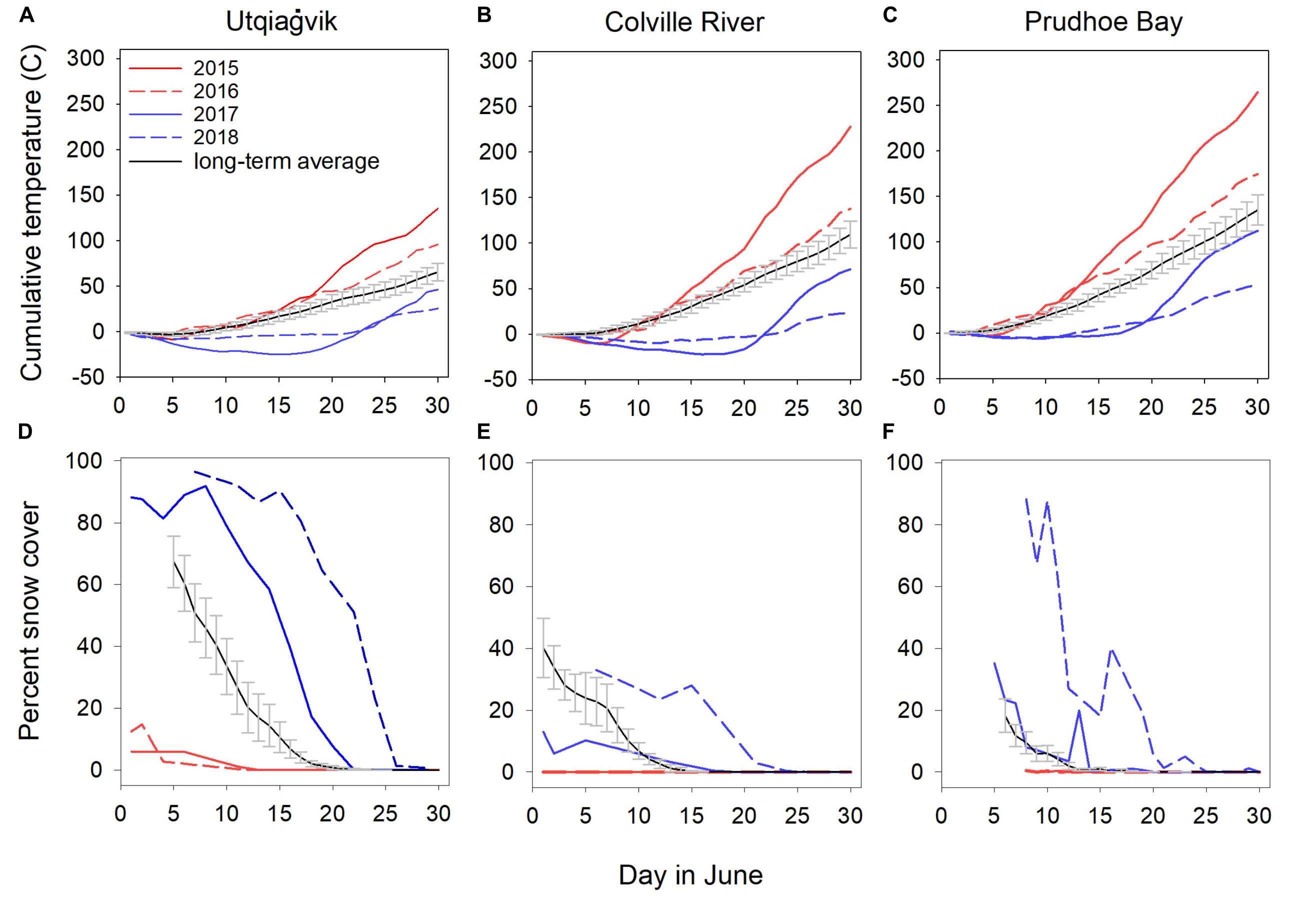

FIGURE 1 | Cumulative daily temperatures and percent snow cover in June, 2015–2018 in relation to the long-term average ± SE [i.e., Utqiaġvik **(A,D)**: 2005–2014; Colville River **(B,E)**: 2005–2014 for temperature, 2011–2014 for snow cover; and Prudhoe Bay **(C,F)**: 2005–2014]. Early springs (i.e., 2015 and 2016) are illustrated in red while late springs (i.e., 2017 and 2018) are illustrated in blue.

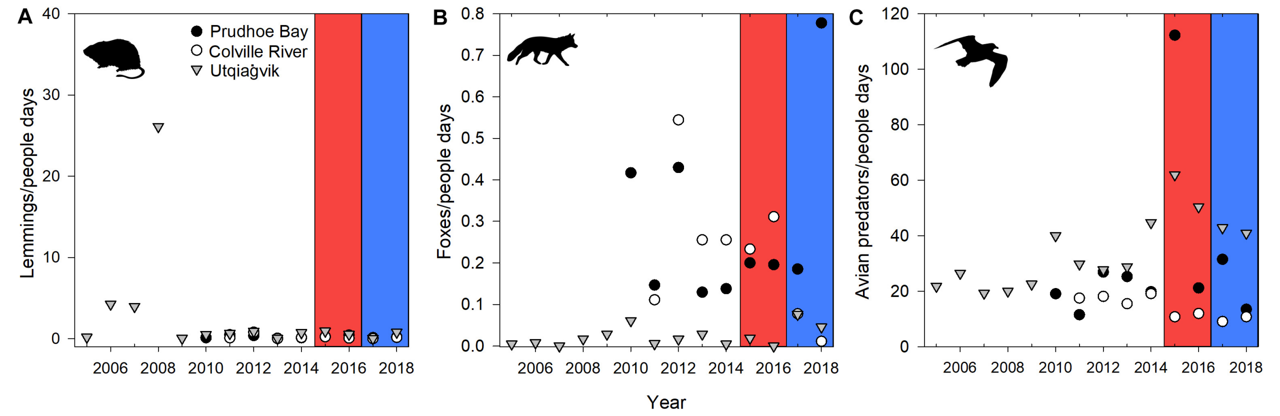

FIGURE 2 | Relative abundance of arvicoline rodents **(A)**, foxes **(B)**, and avian predators **(C)** in June, 2015–2018 in relation to long-term values (i.e., Utqiaġvik: 2005–2014; Colville River: 2011–2014; Prudhoe Bay: 2010–2014). Fox control was in place at Utqiaġvik from 2005 to 2016. Early springs (i.e., 2015 and 2016) are illustrated in red while late springs (i.e., 2017 and 2018) are illustrated in blue.

At Utqiaġvik and Colville River, we investigated phenological mismatch by graphing the area of overlap (a visual representation of the degree of phenological match) between daily invertebrate biomass and the number of broods at their peak energetic demand. To do this, we first estimated predicted hatch date of all nests, regardless of eventual fate, by assuming a 4-egg clutch

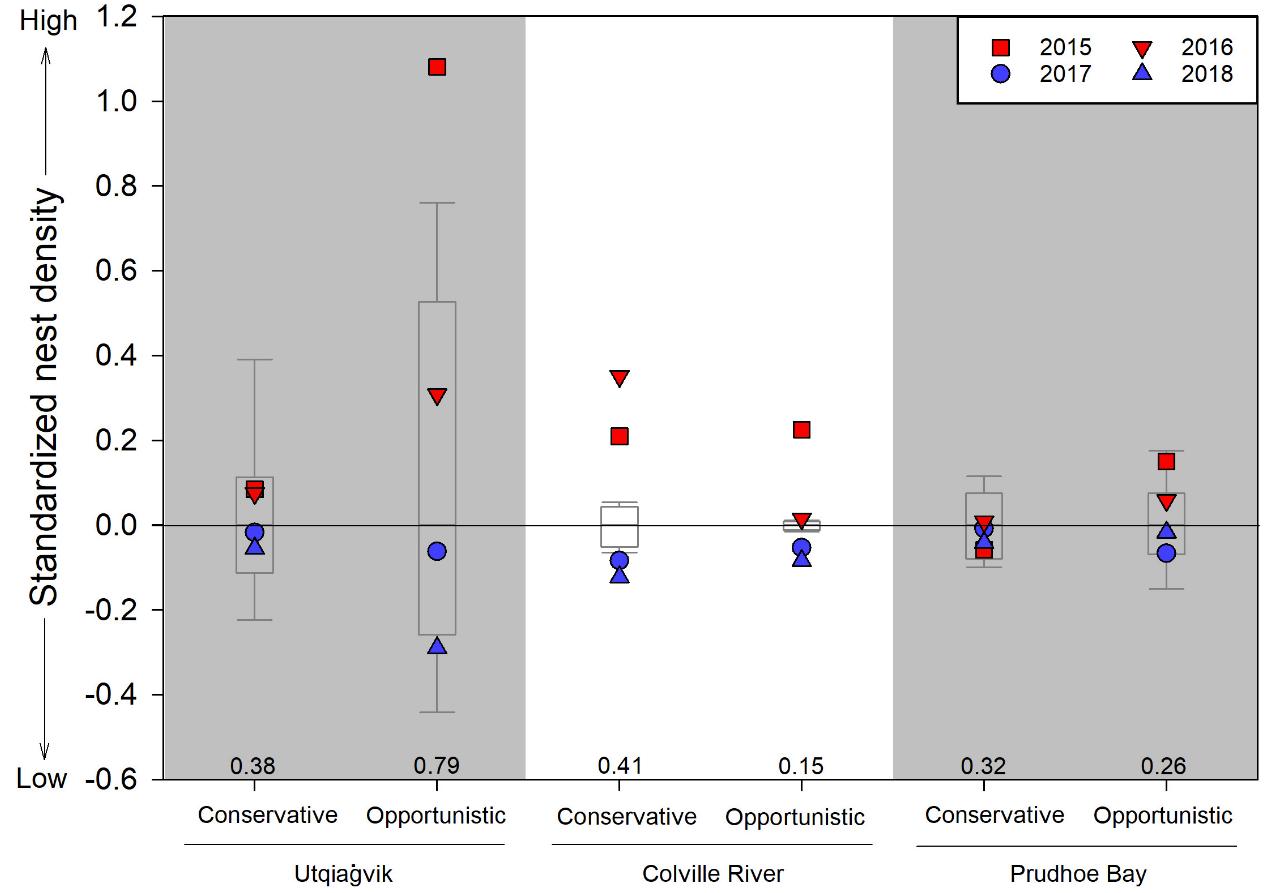

FIGURE 3 | Standardized shorebird nest densities by opportunistic and conservative reproductive strategies in 2015–2018 in relation to long-term values (i.e., Utqiaġvik: 2005–2014; Colville River: 2011–2014; Prudhoe Bay: 2005–2014). Data are standardized for each year and reproductive strategy separately by subtracting from them the long-term median value (median values listed above x-axis); box plots represents the 25th and 75th percentiles with error bars at the 10th and 90th percentiles and the line crossing at the median value. Early springs (i.e., 2015 and 2016) are illustrated in red while late springs (i.e., 2017 and 2018) are illustrated in blue. See **Table 2** for species assignments to reproductive strategies and sample sizes.

with 1 egg laid per day and standard incubation periods. Next, we estimated the number of shorebird broods at their peak energetic demand (i.e., age when chick body mass was 25% of adult body mass after Kwon et al., 2019) for each day of the field season. As our data included several species not included in Kwon et al. (2019) and with little information on growth rates, we chose to use 6 days post-hatch (middle value between 3 and 9 days used by Kwon et al. (2019)) for all species as the date of peak energetic demand. We then graphed the area of overlap between daily invertebrate biomass and the number of broods at their peak energetic demand using the same scale in all cases. All values throughout the paper are reported as means ± standard error.

RESULTS

Weather

The years 2015 and 2016 had considerably warmer temperatures and less snow cover as compared to 2017 and 2018 across all sites (i.e., mean cumulative temperature from 1 to 30 June across sites was 209 ± 39°C in 2015, 136 ± 23°C in 2016, 77 ± 19°C in 2017, and 34 ± 10°C in 2018; mean % snow cover on 10 June across sites was 0.7 ± 0.7% in 2015, 0.3 ± 0.2% in 2016, 30.2 ± 24.3% in 2017, and 69.2 ± 21.3% in 2018; **Figure 1**). Additionally, 2015 and 2016 had consistently warmer temperatures and less snow cover than the long-term average, while 2017 and 2018 had consistently colder temperatures and more snow cover than the long-term average (**Figure 1**). Based on this, we considered 2015 and 2016 as exceptionally early springs and 2017 and 2018 as exceptionally late springs.

Alternative Prey and Predator Abundance

At all sites, the abundance of alternative prey in June was consistently low during the 2015–2018 study period (**Figure 2**). Fox abundance, however, was higher in 2018 at Prudhoe Bay than the first 3 years of this study, while at the Colville River, fox abundance was slightly lower in 2017 and 2018 as compared to 2015 and 2016 (**Figure 2**). At Utqiaġvik, however, fox abundance

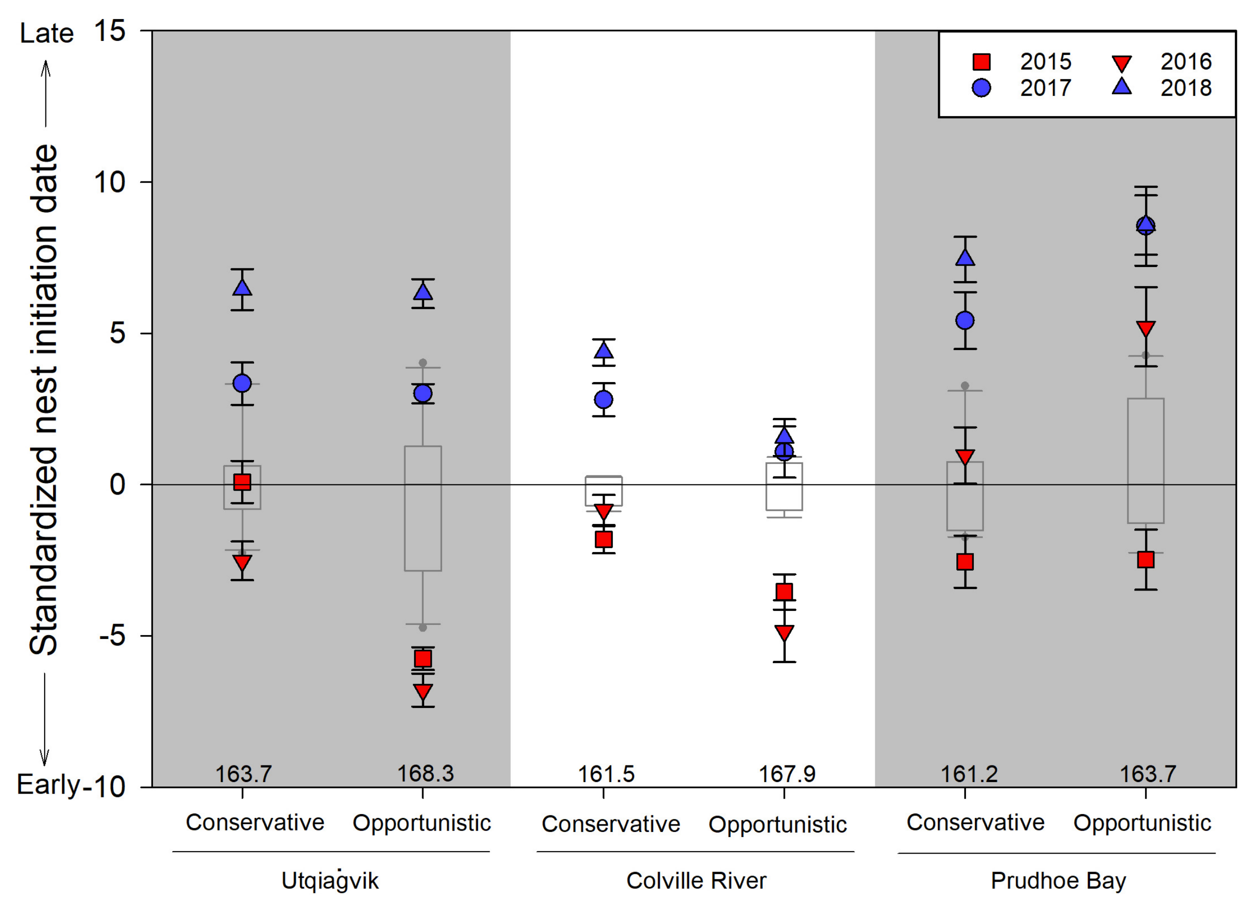

FIGURE 4 | Standardized shorebird nest initiation dates (mean ± SE) by conservative and opportunistic reproductive strategies in 2015–2018 in relation to long-term values (i.e., Utqiaġvik: 2005–2014; Colville River: 2011–2014; Prudhoe Bay: 2005–2014). Data are standardized for each year and reproductive strategy separately by subtracting from them the long-term median value (median values listed above x-axis); box plots represent the 25th and 75th percentiles with error bars at the 10th and 90th percentiles and the line crossing at the median value. Early springs (i.e., 2015 and 2016) are illustrated in red while late springs (i.e., 2017 and 2018) are illustrated in blue. Julian date 150 = 30 May (29 May in leap years). See **Table 2** for species assignments to reproductive strategies and sample sizes.

was fairly consistent and low from 2005 to 2018 despite the fact that an active fox-control program occurred between 2005 and 2016 to promote the reproduction of Steller's Eiders (*Polysticta stelleri*; Barto et al., 2016). Avian predators were generally consistent within sites in the 4 years of this study, except for higher abundances in 2015 at Prudhoe Bay (**Figure 2**). Utqiaġvik generally had 2–3 times the number of avian predators compared to the other sites (except Prudhoe Bay in 2015), with the Colville River having consistently lower numbers.

Nest Densities

Across all sites, we monitored 2,239 nests belonging to 13 species and six genera of shorebirds from 2015 to 2018, and an additional 3,789 nests belonging to 15 species and seven genera from 2005 to 2014 (**Table 2**). The *Calidris* and *Phalaropus* genera were the most common, followed by *Limnodromus, Pluvialis, Arenaria,* and *Limosa*. Nest densities were almost always higher in early springs (11 of 12 site/strategy cases had values above the long-term median value) and lower in late springs (12 of 12 cases) compared to long-term levels (**Figure 3**). The most dramatic differences were seen in opportunistic species at Utqiaġvik, which were found in much higher densities in early (1.49 ± 0.39 nests/ha) compared to late springs (0.62 ± 0.11). The Colville River site had the opposite pattern, where the most dramatic differences were seen in conservative species, which were found in much higher densities in early (0.69 ± 0.07) compared to late (0.31 ± 0.02) springs (**Figure 3**).

Nest Initiation Dates

Nest initiation dates were always earlier in early springs compared to late springs, regardless of the reproductive strategy (**Figure 4**). Furthermore, initiation dates were earlier in 9 of 12 site/strategy cases during earlier springs compared to long-term values. In contrast, initiation dates were always later in late springs (12 of 12 cases) compared to long-term values. The best-supported model mirrored these general patterns, with variation in nest initiation date best explained by the interaction between site, year, and strategy (**Tables 3**, **4**; $R^2 = 0.295$). Within-year comparisons showed opportunistic species nested later than conservative species in 11 of 12 cases.

TABLE 3 | Top-ranked models (plus intercept-only model) explaining variation in initiation dates of shorebird nests at Utqiaġvik, Colville River, and Prudhoe Bay, 2015–2018.

Model	K^a	$AIC_c{}^b$	$\Delta AIC_c{}^c$	$w_i{}^d$
Site × year × strategy	24	14790.6	0.0	1.0
Site × year + strategy	13	14878.5	87.9	0.0
Site × spring × strategy	12	14892.1	101.5	0.0
Year × strategy + site	10	14925.5	134.9	0.0
Year × strategy	8	14939.4	148.8	0.0
Intercept	1	15613.2	822.6	0.0

Variables include site, year, spring (early or late), and reproductive strategy (conservative or opportunistic). We restricted models so that year and spring did not enter the same model. [a]*No. of parameters in the model.* [b]*Akaike's information criterion corrected for small sample size.* [c]*Difference between model AIC_C and AIC_C value of the best model.* [d]*AIC_C relative weight attributed to model.*

Nest Synchrony

In 11 of 12 strategy/site cases, shorebirds nested less synchronously during early springs compared to long-term values, and in 8 of 12 cases, nested more synchronously during late springs compared to long-term values (**Figure 5**). During late springs, opportunistic species nested more synchronously than conservative species at Utqiaġvik and the Colville River, but not at Prudhoe Bay. In contrast, during early springs, opportunistic species nested less synchronously than conservative species at Utqiaġvik and Prudhoe Bay, but not at the Colville River.

Nest Survival

Relative to long-term values, daily nest survival during late springs was lower than the long-term median values in 8 of 12 cases, while daily nest survival was greater than the long-term median values in early springs in just 3 of 12 cases (**Figure 6**). Similarly, our analyses found that variation in daily nest survival was best explained by a model that included site, year, initiation date, and reproductive strategy (**Tables 5**, **6**). Based on this model, both conservative and opportunistic species had greater nest survival in early springs compared to late springs at Utqiaġvik, while opposite trends or no differences between early and late springs were found at the other two sites (**Figure 6**). We also found that daily nest survival declined with initiation date across sites, years, and reproductive strategies ($ß_{\text{initiation}} = -0.04 \pm 0.01$, 95% CI −0.05, −0.03).

Hatch Dates and Invertebrate Abundance

Invertebrate availability was later in late springs than early springs, although there was large variation in the absolute abundance and phenology among years and sites (**Figures 7**, **8**). In early springs, timing of peak food demand for the majority of both conservative and opportunistic broods occurred after peak invertebrate emergence, with less overlap between the two curves (**Figures 7**, **8**, red area). This was especially apparent in 2015 at both Utqiaġvik and the Colville River. In contrast, in late springs, the timing of peak food demand for the majority of broods occurred when invertebrate biomass was more available, with greater overlap between the two curves (**Figures 7**, **8**, blue area).

TABLE 4 | Parameter estimates from top-ranked model (site*year*strategy) explaining variation in initiation dates of shorebird nests at Utqiaġvik, Colville River, and Prudhoe Bay, 2015–2018.

Parameter	Estimate	*SE*
Intercept[a]	172.31	1.21
Site (Utqiaġvik)	2.31	1.37
Site (Colville River)	−2.87	2.03
Year (2015)	−11.07	1.53
Year (2016)	−3.36	1.62
Year (2017)	−0.04	1.85
Strategy (conservative)	−3.64	1.66
Site*year (Utqiaġvik*2015)	−1.00	1.69
Site*year (Colville River*2015)	5.97	2.33
Site*year (Utqiaġvik*2016)	−9.74	1.79
Site*year (Colville River*2016)	−3.03	2.48
Site*year (Utqiaġvik*2017)	−3.27	2.02
Site*year (Colville River*2017)	−0.44	2.80
Site*strategy (Utqiaġvik*conservative)	−0.83	1.95
Site*strategy (Colville River*conservative)	0.13	2.45
Year*strategy (2015*conservative)	1.08	2.24
Year*strategy (2016*conservative)	−3.11	2.25
Year*strategy (2017*conservative)	−1.98	2.44
Site*year*strategy (Utqiaġvik*2015*conservative)	4.63	2.56
Site*year*strategy (Colville River*2015*conservative)	−2.17	2.98
Site*year*strategy (Utqiaġvik*2016*conservative)	7.25	2.59
Site*year*strategy (Colville River*2016*conservative)	4.30	3.06
Site*year*strategy (Utqiaġvik*2017*conservative)	2.18	2.80
Site*year*strategy (Colville River*2017*conservative)	0.89	3.38

Variables include site, year, and reproductive strategy (conservative or opportunistic). [a]*Intercept represents estimates for nests at Prudhoe Bay in 2018 with an opportunistic reproductive strategy.*

DISCUSSION

In our multi-species assessment of the demographic response of Arctic-breeding shorebirds to variable spring conditions across three sites in Alaska, many results clearly fit our predictions and involved birds making adjustments that are perceived as adaptive responses to prevailing environmental conditions (**Table 1**). Such results were not wholly surprising, because our predictions were based on a wealth of prior studies investigating these relationships (see introduction). The most interesting results of this study, then, concern those that did not fit our predictions. For example, we observed strong differences among sites in the magnitude (e.g., nest density; **Figure 3**) and direction (e.g., nest initiation and nest synchrony responses among conservative and opportunistic species; **Figures 4**, **5**) of certain demographic responses. Given the close proximity and similarity of habitats across our three study sites, this was unexpected. It is possible that some variation in our response variables was present due to the potential effects of fox control at Utqiaġvik, human infrastructure at Prudhoe Bay and Utqiaġvik, or subtle differences in other ecological variables that we did not measure (e.g., hydrology, geomorphology). Notably, inter-site variation in the abundance of alternative prey or avian and mammalian nest predators seems unlikely to have driven these patterns, because the abundance of

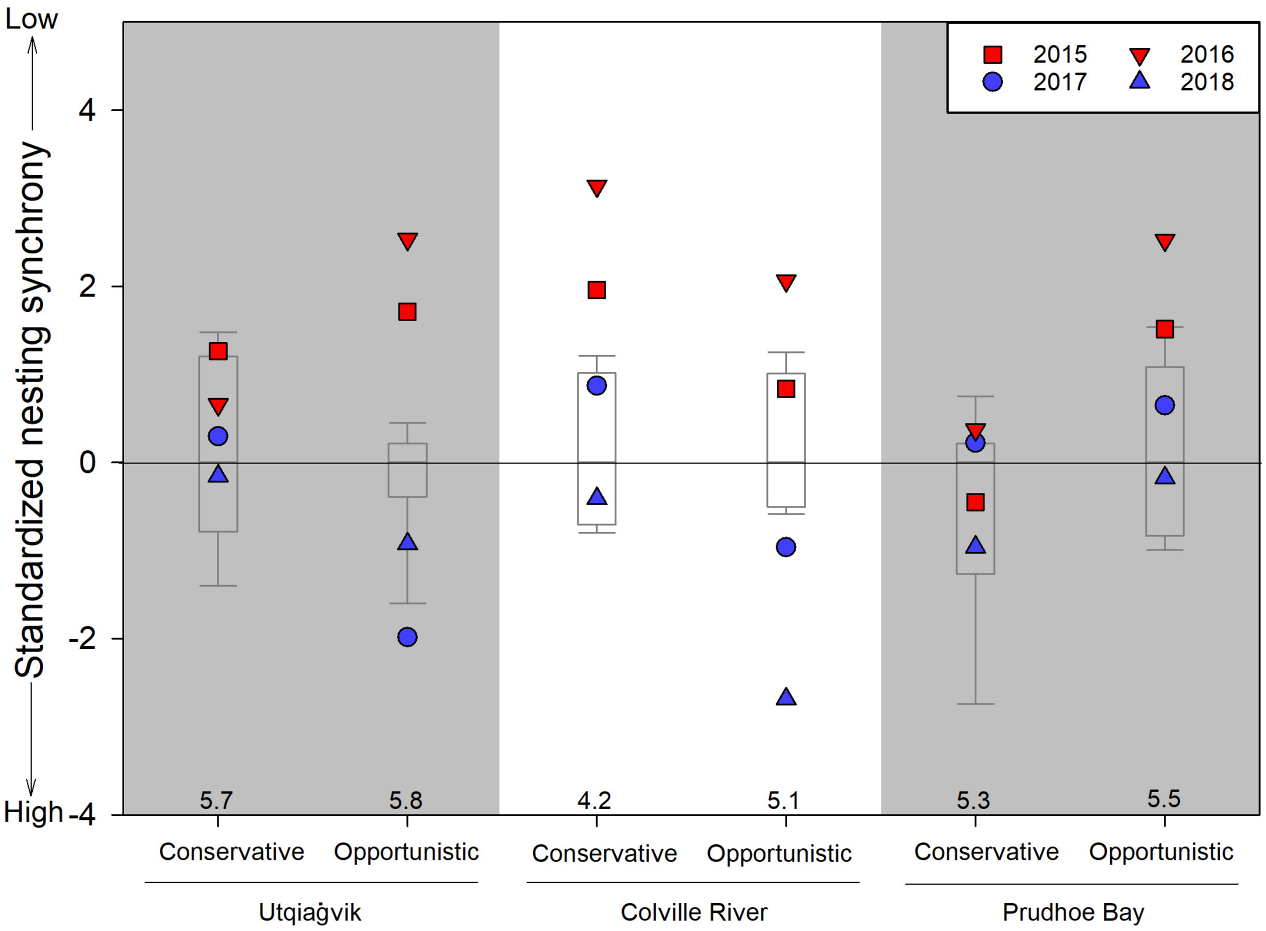

FIGURE 5 | Standardized shorebird nest synchrony (standard deviation of nest initiation dates, after Nol et al., 1997) by opportunistic and conservative reproductive strategies in 2015–2018 in relation to long-term values (i.e., Utqiaġvik: 2005–2014; Colville River: 2011–2014; Prudhoe Bay: 2005–2014). Data are standardized for each year and reproductive strategy separately by subtracting from them the long-term median value (median values listed above x-axis); box plots represent the 25th and 75th percentiles with error bars at the 10th and 90th percentiles and the line crossing at the median value. Early springs (i.e., 2015 and 2016) are illustrated in red while late springs (i.e., 2017 and 2018) are illustrated in blue. Smaller values indicate greater nest synchrony. See **Table 2** for species assignments to reproductive strategies and sample sizes.

alternative prey was low at all sites in all years, and the relatively high numbers of mammalian and avian predators at some sites and years were not associated with nest survival in a consistent and predictable way (**Table 1**).

There were small methodological differences among the sites that might have contributed to different results among study sites. Our sites had different numbers and sizes of plots (e.g., many small linear plots versus six square plots versus one large plot), plots were searched for nests at different frequencies and with different approaches (timing, order and use of area search versus rope-drag techniques), and each site had different numbers of long-term years with which to compare the early and late spring information. These differences may influence the likelihood of finding nests (e.g., see McCaffery and Ruthrauff, 2004; Smith et al., 2009) and potentially affect perceptions of how reproductive parameters may change in early and late springs. Given the sheer number of nesting efforts monitored across these sites during our studies, however, we do not believe that these methodological differences account for magnitude of the demographic differences observed across sites. A more striking difference between the sites, however, was the difference in the shorebird community structure and the absolute numbers of particular species. For, example, opportunistic species (e.g., Red Phalarope and Pectoral Sandpiper) were dominant at Utqiaġvik, while conservative species (e.g., Semipalmated Sandpiper, Dunlin) were dominant at the Colville River; the shorebird community at Prudhoe Bay was more balanced (**Table 2**). These differences in community composition might explain why Utqiaġvik followed the predictions for opportunistic species more closely than the other sites (**Table 1**).

Our prediction that nest densities for conservative species would not change in early springs compared to the long-term median value was not supported at the Utqiaġvik and Colville River sites (both sites increased between 0.08 and 0.35 nests/ha), but was supported at Prudhoe Bay (**Figure 3**). However, our prediction that opportunistic species would nest in higher

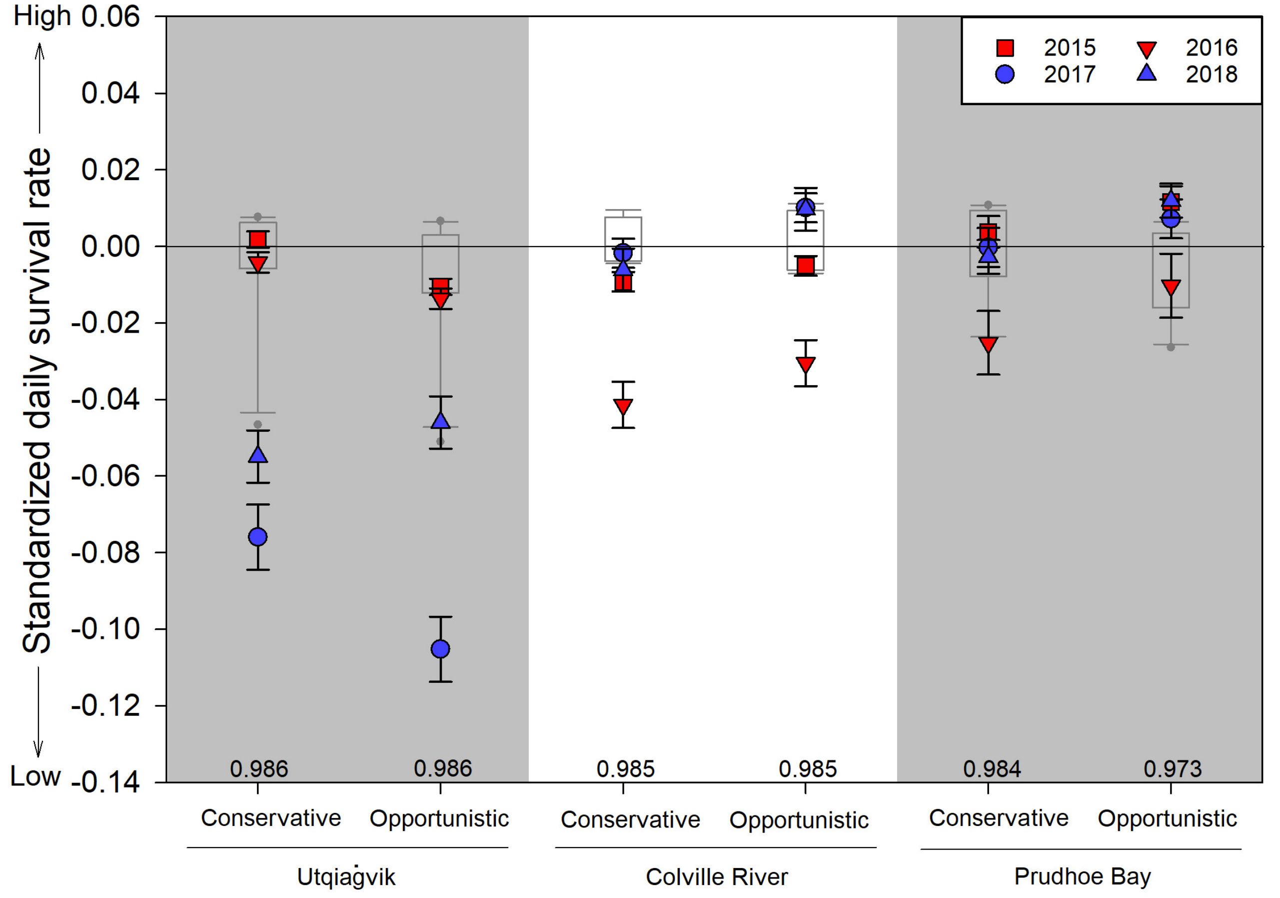

FIGURE 6 | Standardized daily survival rate ± SE of shorebird nests by conservative and opportunistic reproductive strategies in 2015–2018 in relation to long-term values (i.e., Utqiaġvik: 2005–2014; Colville River: 2011–2014; Prudhoe Bay: 2005–2014). Data are standardized for each year and reproductive strategy separately by subtracting from them the long-term median value (median values listed above x-axis); box plots represent the 25th and 75th percentiles with error bars at the 10th and 90th percentiles and the line crossing at the median value. Early springs (i.e., 2015 and 2016) are illustrated in red while late springs (i.e., 2017 and 2018) are illustrated in blue. Values estimated for mean nest initiation date (i.e., 14 June, 13 June in leap years) based on parameter estimated from the top-ranked model (Daily nest survival $_{site*year*strategy\ +initiation}$). See **Table 2** for species assignments to reproductive strategies and sample sizes.

densities in early springs was met at all three study sites. This was especially notable at Utqiaġvik, where nest densities of opportunistic species were 0.31 to 1.1 nests/ha greater in early springs compared to long-term levels. Some of the increase in nest density during early springs may be due to birds laying replacement nests, but this seems unlikely to account for the large increases in nest density for opportunistic species at Utqiaġvik and conservative species at the Colville River. Following our prediction, both conservative and opportunistic species nested at lower densities during late springs, although the decline in nesting density was very small (<0.29 nests/ha) compared to long-term levels. In fact, in several years and at multiple sites, nest density was not affected at all. Changes in nest density were generally absent at Prudhoe Bay, regardless of reproductive strategy and the type of spring. While it is difficult to know the extent of replacement nesting (detailed mark-resight or paternity investigations are needed), it is likely that social cues that either limit conspecific nesting (Cunningham et al., 2016) or enhance it are important (Kempenaers and Valcu, 2017). Most of our results support past assertions that opportunistic species are able to adjust to spring conditions better than conservative species, presumably due to their ability to assess conditions over large portions of their breeding range (Lanctot and Weatherhead, 1997; Kempenaers and Valcu, 2017). However, other assertions that birds are unable to breed during late springs due to the inability to acquire the necessary exogenous reserves (Nol et al., 1997; Meltofte et al., 2007b; Smith et al., 2010) seem less supported, as nest densities remained near long-term levels during these exceptionally late springs (except for at Utqiaġvik). It is possible that the late spring conditions experienced in some of our study areas were not sufficiently poor to inhibit breeding efforts as has been reported at other sites (see, e.g., Schmidt et al., 2019).

Other studies have shown that Arctic-breeding shorebirds align the timing of nest initiation, although not always as fast as necessary, with the availability of snow-free habitats (Meltofte et al., 2007a; Smith et al., 2010; Grabowski et al., 2013; Liebezeit et al., 2014; Machín et al., 2019). Kwon et al. (2019) likewise found

TABLE 5 | Top-ranked models (plus intercept-only model) explaining daily survival rates of shorebird nests at Utqiaġvik, Colville River, and Prudhoe Bay, 2015–2018.

Model	K^a	$AIC_c{}^b$	$\Delta AIC_c{}^c$	$w_i{}^d$
Site × year × strategy + initiation	25	4887.1	0.0	0.6
Site × year × initiation	24	4889.6	2.6	0.2
Site × year + initiation	13	4889.9	2.8	0.1
Site × year + initiation + strategy	14	4890.2	3.1	0.1
Site × year + strategy	13	4927.5	40.4	0.0
Site × year × strategy	24	4928.0	40.9	0.0
Site × year	12	4933.3	46.2	0.0
Intercept	1	5381.5	494.4	0.0

Variables include site, year, spring (early or late), reproductive strategy (conservative or opportunistic), and nest initiation date. We restricted models so that year and spring did not enter the same model. [a]*No. of parameters in the model.* [b]*Akaike's information criterion corrected for small sample size.* [c]*Difference between model AIC_c and AIC_c value of the best model.* [d]*AIC_c relative weight attributed to model.*

TABLE 6 | Parameter estimates from top-ranked model (site*year*strategy + initiation) explaining variation in daily survival rates of shorebird nests at Utqiaġvik, Colville River, and Prudhoe Bay, 2015–2018.

Parameter	Estimate	*SE*
Intercept (Utqiaġvik*2015)	4.27	0.14
Intercept (Utqiaġvik*2016)	4.15	0.15
Intercept (Utqiaġvik*2017)	2.58	0.16
Intercept (Utqiaġvik*2018)	3.33	0.19
Intercept (Colville River*2015)	4.46	0.21
Intercept (Colville River*2016)	3.62	0.23
Intercept (Colville River*2017)	5.86	0.72
Intercept (Colville River*2018)	5.79	1.01
Intercept (Prudhoe Bay*2015)	4.74	0.37
Intercept (Prudhoe Bay*2016)	3.83	0.28
Intercept (Prudhoe Bay*2017)	4.49	0.44
Intercept (Prudhoe Bay*2018)	4.77	0.38
Strategy (Utqiaġvik*2015*conservative)	0.73	0.25
Strategy (Utqiaġvik*2016*conservative)	0.44	0.24
Strategy (Utqiaġvik*2017*conservative)	0.32	0.17
Strategy (Utqiaġvik*2018*conservative)	−0.15	0.19
Strategy (Colville River*2015*conservative)	−0.20	0.23
Strategy (Colville River*2016*conservative)	−0.23	0.23
Strategy (Colville River*2017*conservative)	−1.23	0.75
Strategy (Colville River*2018*conservative)	−1.39	1.03
Strategy (Prudhoe Bay*2015*conservative)	0.19	0.62
Strategy (Prudhoe Bay*2016*conservative)	−0.12	0.39
Strategy (Prudhoe Bay*2017*conservative)	0.17	0.55
Strategy (Prudhoe Bay*2018*conservative)	−0.25	0.51
Initiation	−0.04	0.01

Variables include site, year, reproductive strategy (conservative or opportunistic), and nest initiation date.

that despite differences in ecological and physical environments outside the breeding grounds, shorebirds at 10 sites spread across the Arctic responded to the timing of snowmelt on the breeding grounds by adjusting the timing of breeding in similar ways. None of these studies, however, assessed how reproductive strategy influenced the timing of nesting. Our prediction that birds would nest earlier in early springs and later in late springs was generally supported in this study. We found that shorebirds initiated egg laying earlier in early springs relative to long-term values in most cases (4 of 6 conservative/sites, 5 of 6 opportunistic/sites); the rest nested at the same time or later than long-term values (**Figure 4**). In contrast, in late springs, both conservative and opportunistic species always initiated nests later than long-term values. Within a year and site, opportunistic species nested later than conservative species in 11 of 12 cases. Thus, birds adjusted less reliably to early springs than late springs in this study, but opportunistic species always nested later than conservative species regardless of spring type. We suspect that the need to attract or compete for mates may delay nesting in opportunistic species whereas the site faithfulness of conservative species may allow them to relocate their old mate much faster (Lanctot et al., 2000). In addition, the uniparental incubation patterns present in opportunistic species may impose higher anticipatory energetic costs (Drent et al., 2006) that results in longer pre-breeding delays in nesting compared to conservative species. In contrast, conservative species that practice bi-parental incubation can anticipate more time to feed during incubation (i.e., they can lay eggs despite potentially being in worse body condition). In addition, opportunistic species may end up breeding later in late springs because their arrival is delayed due to their attempts to breed in other parts of the Arctic experiencing earlier spring conditions (Kempenaers and Valcu, 2017). The conservative species, in contrast, go to a single site and wait to initiate nests as soon as habitat opens.

Like many Arctic-breeding birds (e.g., Custer and Pitelka, 1977; Findlay and Cooke, 1982), shorebirds tend to breed synchronously, perceived both as a response to help dilute the individual risk of nest predation (Smith et al., 2010), but also to time the hatching of their young to match future peaks in food resources (Holmes and Pitelka, 1968). However, the warmer and longer breeding seasons that are a byproduct of earlier springs may lengthen the nesting period as shorebirds not only nest earlier but also have more time to renest should their first nest fail. Such a situation effectively decreases the synchrony of nesting events in early springs. While we had little information to confirm the presence of renests, prior research from Utqiaġvik indicates that virtually all shorebirds renest (Naves et al., 2008) and that for Dunlin in particular, renesting can occur at a high frequency (82–95 and 35–50% of nests whose clutches were experimentally removed during early and late incubation, respectively, subsequently renested; Gates et al., 2013). In contrast, later springs are thought to lead to more synchronous nesting, likely due to the shorter period of time in which birds have to nest (Nol et al., 1997; Meltofte et al., 2007b; Smith et al., 2010). These patterns, as outlined above and in our initial predictions, were mostly confirmed in our study, with nesting being less synchronous in early springs (11 of 12 strategy/year cases) and more synchronous in late springs (8 of 12 strategy/year cases) relative to historic levels (2005–2014; **Figure 5**). However, we did not find consistent patterns in nest synchrony between conservative and opportunistic species within years and sites. Collectively these results suggest that, at least across these three sites, the extent to which shorebirds nested

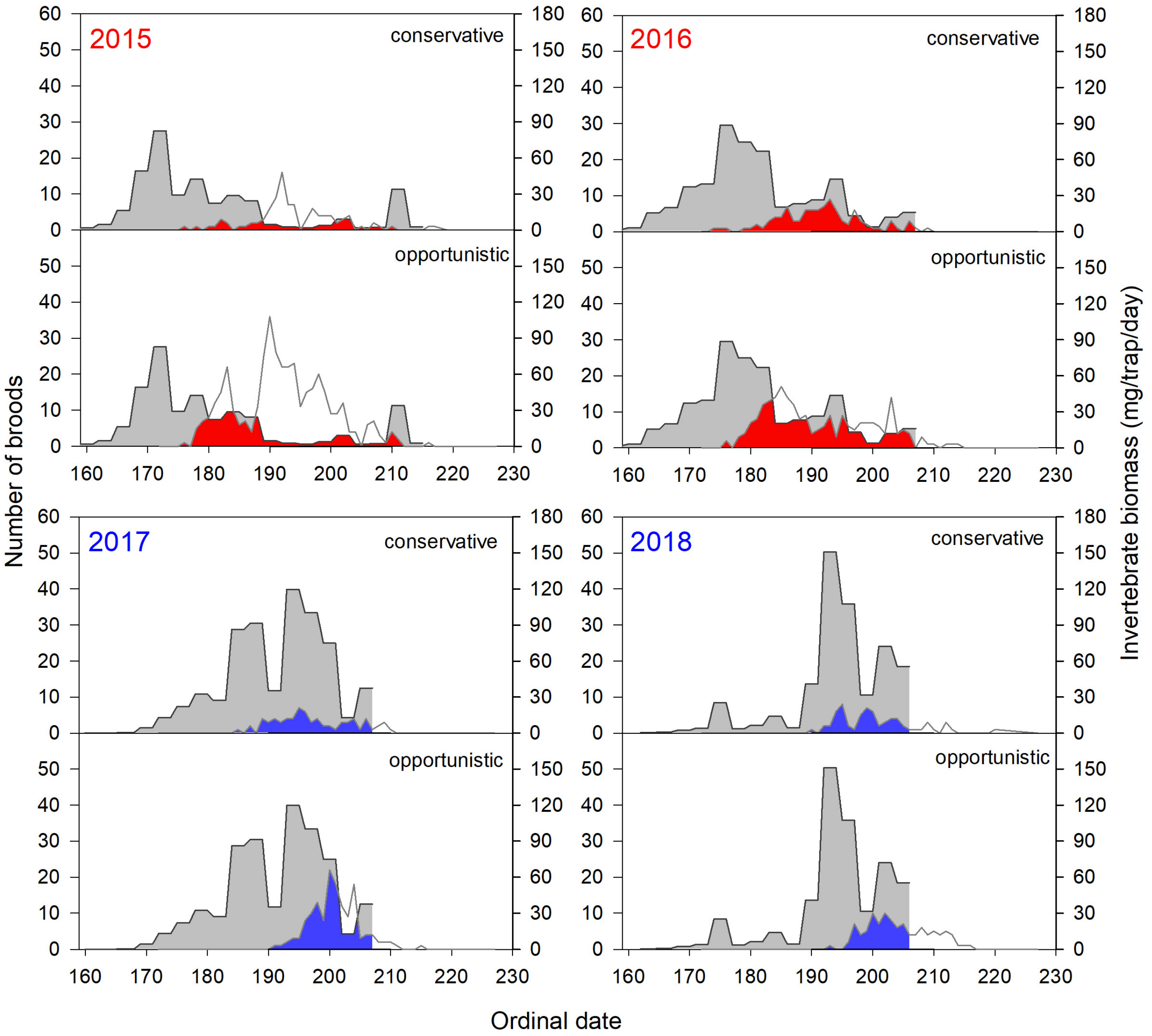

FIGURE 7 | Daily invertebrate biomass (gray) in relation to the number of conservative and opportunistic shorebird broods at peak energetic demand (i.e., 6 days post-hatch) in 2015–2018 at Utqiaġvik. The area of overlap between the two curves (red in early springs 2015 and 2016; blue in late springs 2017 and 2018) illustrates the temporal degree of phenological match. The area outlined in white above red and blue areas reflects additional broods that were 6 days old. In most years, invertebrate sampling ended prior to the end of the brood rearing season (ordinal date 215, 207, 207, and 206 in 2015–2018, respectively); therefore, phenological match cannot be assessed for broods after these time periods. See **Table 2** for species assignments to reproductive strategies and sample sizes.

synchronously was based primarily on the type of spring and not the reproductive strategy of the species.

We predicted that shorebirds would have higher nesting success in early springs compared to late springs. Contrary to our predictions, we found only a few site/year cases where these predicted relationships were followed (**Figure 6**). For example, as predicted, nest survival was lower in the late springs of 2017 and 2018 at Utqiaġvik compared with historic levels. However, these two springs occurred after fox control was stopped in 2016, and it seems possible that higher (i.e., natural) fox densities present in subsequent years might have lowered nest survival (and not the late springs). Our consistently low counts of fox at Utqiaġvik between 2005 and 2018 (**Figure 2**) do not support this idea, although it is possible that our opportunistic counts do not accurately reflect fox activity in the area (see Liebezeit and Zack, 2008). In most site/year cases, however, nest survival was not related to spring type in the ways that we predicted. This was particularly true for the Colville River and Prudhoe Bay sites in the early spring of 2016, when nest survival was lower than the historic levels despite having an early spring. The failure to document lower nest survival in late springs may be because the persistent snow cover not only reduced available

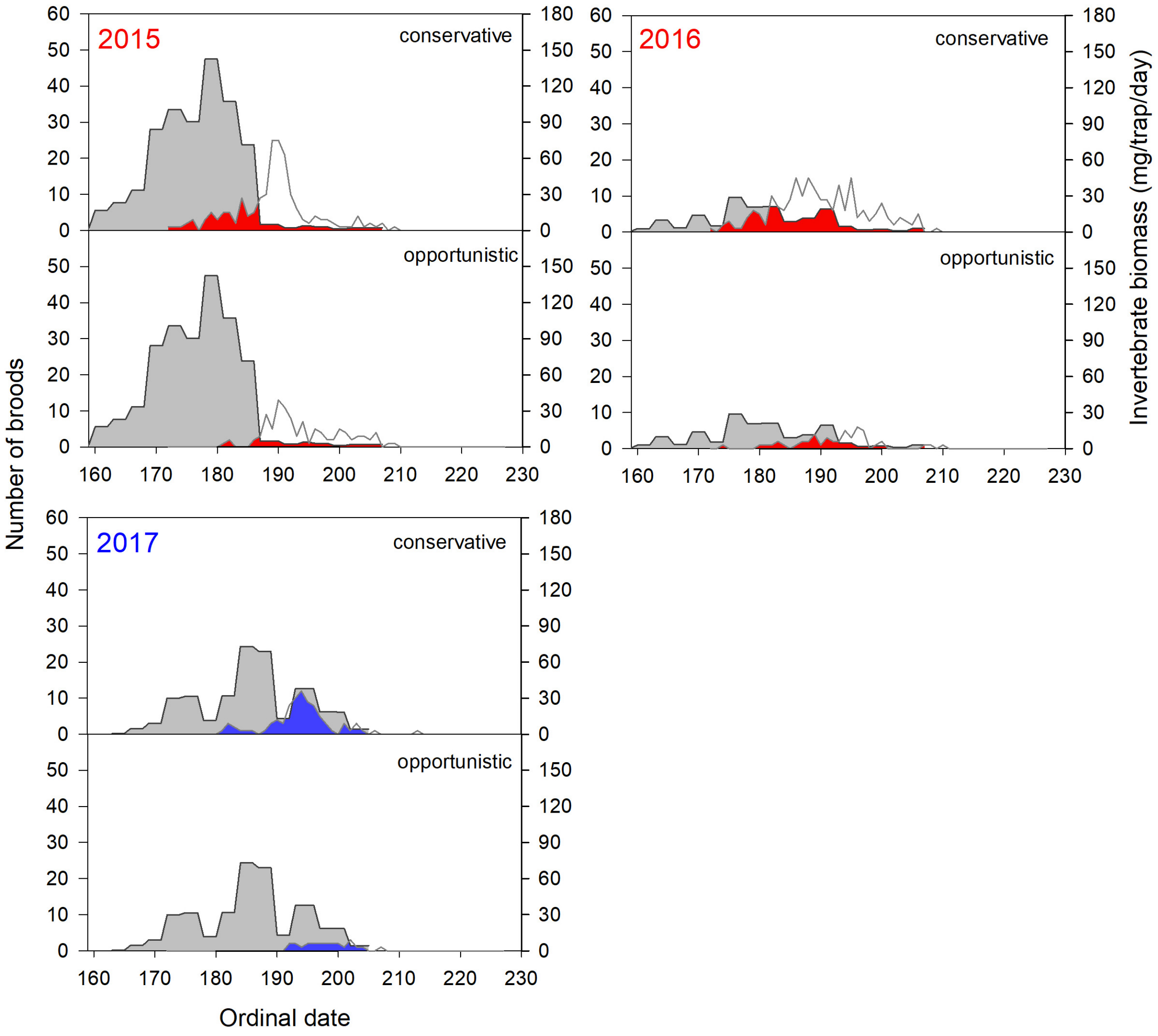

FIGURE 8 | Daily invertebrate biomass (gray) in relation to the number of conservative and opportunistic shorebird broods at peak energetic demand (i.e., 6 days post-hatch) in 2015–2017 at Colville River. The area of overlap between the two curves (red in early springs 2015 and 2016; blue in late spring 2017) illustrates the temporal degree of phenological match. The area outlined in white above red and blue areas reflects additional broods that were 6 days old. In most years, invertebrate sampling ended prior to the end of the brood rearing season (ordinal date 207, 207, and 205 in 2015–2017, respectively); therefore, phenological match cannot be assessed for broods after these time periods. See **Table 2** for species assignments to reproductive strategies and sample sizes.

habitat for nesting (which could concentrate predation intensity) but also resulted in lower overall densities of breeding shorebirds, decreasing nest encounter rates by predators. If encounter rates are sufficiently low, foxes may choose to hunt elsewhere.

Regardless of the spring type, we found a consistent decline in daily nest survival with nest initiation date, suggesting some selective pressure exists to nest as early as possible. Failing to breed early may lead to smaller clutch sizes, less renesting, and ultimately lower adult survival (Weiser et al., 2018b), but breeding early may also be detrimental should predation intensity be greater early in the spring (Reynolds, 1987; Reneerkens et al., 2016). Interestingly, a seasonal decline in nest survival has been found in some studies (Sandercock et al., 1999; Weiser et al., 2018b), but not others (e.g., Smith and Wilson, 2010; Reneerkens et al., 2016; Senner et al., 2017), and so selection pressures likely operate differently across years and sites. This is unsurprising, given that nest survival is primarily driven by both predators and the availability of alternative prey to shorebird predators (Blomqvist et al., 2002; Smith et al., 2007; Gilg and Yoccoz, 2010; McKinnon et al., 2014; Reneerkens et al., 2016), which can vary tremendously from site to site and year to year (Liebezeit et al., 2009; Saalfeld and Lanctot, 2015).

Early springs often resulted in more broods hatching after peak food availability (**Figures 7, 8**). Kwon et al. (2019) also found that site-specific timing of snowmelt determined the extent of phenological mismatches at the population level for six species of shorebirds breeding across the North American Arctic. However, it remains unclear whether this increased temporal asynchrony is harmful to young. McKinnon et al. (2013) and Corkery et al. (2019) both reported chicks growing sufficiently well even under depressed food conditions caused by phenological mismatch, perhaps due to lower thermoregulatory needs during the warmer springs. In contrast, Saalfeld et al. (2019) found that shorebirds experienced increased phenological mismatch with earlier snowmelt, and that, in general, chicks that hatched from nests initiated earlier experienced greater food availability and grew at faster rates than chicks from nests that hatched later. Hill (2012) confirmed that insect biomass was a strong predictor of chick survival in Dunlin. Thus, it is still unclear whether hatching after peak invertebrate availability is disadvantageous, as it likely depends on overall food abundance and weather conditions during a given breeding season.

Overall, our study demonstrates that Arctic-breeding shorebirds exhibit a high degree of behavioral flexibility in response to variable Arctic conditions. Similar adaptability has been documented in a wide variety of organisms from terrestrial and marine ecosystems from around the globe (Parmesan and Yohe, 2003; Hickling et al., 2006; Chen et al., 2011; Poloczanska et al., 2013), but such adjustments have been recognized only relatively recently in shorebirds (e.g., Liebezeit et al., 2014; Kwon et al., 2019). It is necessary to determine whether existing behavioral flexibility in nesting is already sufficient to keep pace with advancing Arctic phenologies (Berteaux et al., 2004; Williams et al., 2008), or whether additional evolutionary adjustments (e.g., Hoffmann and Sgrò, 2011; Helm et al., 2019) will be required. It is important to understand these relationships given change is continuing to happen (Schmidt et al., 2019) and the potential impacts are large (see, e.g., Wauchope et al., 2016). Such information will better articulate life-history attributes that may buffer migratory birds against extreme environmental events (Williams et al., 2008).

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: "Data from the Colville River used in this study are publicly available from the U.S. Geological Survey (https://doi.org/10.5066/P9BJBRTO). Data for Utqiaġvik are available from the Arctic Data Center (https://doi.org/10.18739/A23R0PT35). The raw data from Prudhoe Bay will be made available by the authors upon request."

ETHICS STATEMENT

The animal study was reviewed and approved by Colville River Site: US Geological Survey/Alaska Science Center Institutional Care and Use Committee. Prudhoe Bay Site: Alaska Department of Fish and Game Institutional Care and Use Committee. Utqiaġvik Site: US Fish and Wildlife Service Alaska Region Institutional Care and Use Committee.

AUTHOR CONTRIBUTIONS

RM, RL, SS, and DR conceptualized the study. RM and SS analyzed the data. RM wrote the manuscript. RL, SS, and DR contributed significantly to data interpretation and writing. All authors approved the final manuscript and collected the data.

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Not Singing in the Rain: Linking Migratory Songbird Declines With Increasing Precipitation and Brood Parasitism Vulnerability

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Few empirical studies have quantified relationships between changing weather and migratory songbirds, but such studies are vital in a time of rapid climate change. Climate change has critical consequences for avian breeding ecology, geographic ranges, and migration phenology. Changing precipitation and temperature patterns affect habitat, food resources, and other aspects of birds' life history strategies. Such changes may disproportionately affect species confined to rare or declining ecosystems, such as temperate grasslands, which are among the most altered and endangered ecosystems globally. We examined the influence of changing weather on the dickcissel (*Spiza americana*), a migratory songbird of conservation concern that is an obligate grassland specialist. Our study area in the North American Great Plains features high historic weather variability, where climate change is now driving higher precipitation and temperatures as well as higher frequencies of extreme weather events including flooding and droughts. Dickcissels share their breeding grounds with brown-headed cowbirds (*Molothrus ater*), brood parasites that lay their eggs in the nests of other songbirds, reducing dickcissel productivity. We used 9 years of capture-recapture data collected over an 18-year period to test the hypothesis that increasing precipitation on dickcissels' riparian breeding grounds is associated with abundance declines and increasing vulnerability to cowbird parasitism. Dickcissels declined with increasing June precipitation, whereas cowbirds, by contrast, increased. Dickcissel productivity appeared to be extremely low, with a 3:1 ratio of breeding male to female dickcissels likely undermining reproductive success. Our findings suggest that increasing precipitation predicted by climate change models in this region may drive future declines of dickcissels and other songbirds. Drivers of these declines may include habitat and food resource loss related to flooding and higher frequency precipitation events as well as increased parasitism pressure by cowbirds. Positive correlations of June-July precipitation, temperature, and time since grazing with dickcissel productivity did not mitigate dickcissels' declining trend in this ecosystem. These findings highlight the importance of empirical research on the effects of increasing precipitation and brood parasitism vulnerability on migratory songbird conservation to inform adaptive management under climate change.

Keywords: climate change, weather, grassland breeding birds, Monitoring Avian Productivity and Survivorship (MAPS), grazing, haying, dickcissel (*Spiza americana*), brown-headed cowbird (*Molothrus ater*)

INTRODUCTION

Global climate change is influencing birds' breeding ecology, geographic ranges, and migration phenology. Changing precipitation and temperature patterns affect birds directly as well as indirectly through their impacts on habitat, food resources, and other factors critical to avian life history strategies and population dynamics (Moss et al., 2001; Cotton, 2003; Niemuth et al., 2008; Knudsen et al., 2011; McDonald et al., 2012; López-Calderón et al., 2019). For example, precipitation declines on the breeding grounds of yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) have been correlated with density declines and reproductive failure (Fletcher and Koford, 2004). For burrowing owls (*Athene cunicularia*), precipitation declines and higher temperatures on the breeding grounds were associated with delayed arrival dates and lower abundance and productivity, resulting in population collapse (Cruz-McDonnell and Wolf, 2016). For whooping cranes (*Grus americana*), precipitation declines and higher temperatures on the breeding grounds are predicted to drive declines in juvenile recruitment by increasing their vulnerability to mammalian nest predators, driving population-wide declines (Butler et al., 2017). In addition to the influence of changing precipitation and temperature on the breeding grounds, climatic conditions on birds' migration routes and wintering grounds may also influence bird population dynamics, including through carry-over effects that exert influence in multiple seasons (Marra et al., 1998; Finch et al., 2014; O'Connor et al., 2014; Akresh et al., 2019). Climate change effects may vary considerably within and across geographic regions (e.g., USGCRP, 2018), carrying the potential to affect local bird populations differently across geographic gradients (e.g., Jensen and Cully, 2005).

Climate change may disproportionately affect species restricted to rare or declining ecosystems, such as temperate grasslands, which are among the most endangered and least protected ecosystems worldwide (White et al., 2000; Blancher, 2003). In North America, >80% of temperate grasslands have been converted to agriculture and other human uses (With et al., 2008), driving bird declines (Pietz and Granfors, 2000; Brennan and Kuvlesky, 2005; Stanton et al., 2018). North American grassland birds have declined >50% in abundance in the past 50 years (Askins et al., 2007; Sauer et al., 2012; Rosenberg et al., 2019), warranting urgent conservation attention. Few empirical studies have examined impacts of weather on grassland bird populations (Amburgey et al., 2018; Kleinhesselink and Adler, 2018; Scridel et al., 2018). However, some research to date has identified positive correlations between precipitation levels and grassland bird abundance, productivity, and recruitment (e.g., Patterson and Best, 1996; Rahmig et al., 2009). For example, winter grassland songbird density in desert grasslands in Mexico has been positively correlated with precipitation the preceding year, which in turn was associated with higher grass productivity (Macías-Duarte et al., 2009). In riparian grasslands, however, while increased precipitation may be associated with increased habitat quality in uplands, it may also be correlated with local flooding and lower bird abundance (Kim et al., 2008; Glass et al., 2020), lower arthropod food availability (Siikamäki, 1996; Plum, 2005; Sienkiewicz and Żmihorski, 2012), and lower productivity (Skagen and Yackel Adams, 2012; Jarzyna et al., 2016).

Far removed from the ocean's moderating effects on weather, the North American Great Plains are prone to dramatic climate variability (Skagen and Yackel Adams, 2012; Conant et al., 2018; USGCRP, 2018), making this an ideal region in which to explore the effects of weather on grassland birds. The "climate bottleneck hypothesis" predicts that precipitation extremes should not influence grassland breeding bird abundance as long as grasslands retain sufficient structural complexity because obligate grassland birds have evolved to tolerate extreme weather events (Wiens, 1974; Zimmerman, 1992). A 10-year study found support for this hypothesis, showing that obligate grassland bird abundance did not change in response to precipitation levels during a period when extreme weather events such as floods or droughts occurred approximately once every 4 years (Zimmerman, 1992). In riparian grasslands, however, which are drought-resistant but flood-prone, studies have found higher levels of precipitation correlated with lower local abundances of grassland birds (Kim et al., 2008; Glass et al., 2020). Climate change is introducing unprecedented variability in extreme weather events in the eastern Great Plains, with expected increases in the number of days with heavy (>2.5 cm) precipitation and an increasing number (15–40) of very hot (>32°C) days (USGCRP, 2018). Examining how precipitation and temperature influence grassland breeding bird populations in this region is crucial for advancing our understanding of their ecology and informing conservation efforts under future climate change.

Obligate grassland specialists, dickcissels (*Spiza americana*) are sensitive to temperature and moisture changes throughout the annual cycle, making them excellent indicators of weather and climate change effects on grassland bird populations (DeSante et al., 2015; Culp et al., 2017). Neotropical migratory birds, dickcissels' core nesting grounds are in the North American Great Plains and their core wintering grounds are in Venezuela (Sauer et al., 2005; Temple, 2020). Dickcissels underwent severe declines in the mid-20th century and have not recovered their previous numbers (Temple, 2020). Recent (1992–2006) data from both the North American Breeding Bird Survey (BBS) and the Monitoring Avian Productivity and Survivorship (MAPS) program showed dickcissel populations as stable, albeit with a non-significant declining trend (DeSante et al., 2015). However, dickcissels remain highly vulnerable to extinction due to habitat loss and other anthropogenic impacts that have already reduced and fragmented their populations (Culp et al., 2017). Dickcissel nest success tends to be low, with past studies reporting that 29–44% of nesting females produced only ∼1 fledgling/season (Zimmerman, 1982; Basili et al., 1997). Females take sole responsibility for nest building, incubation, and caring for young (Temple, 2020). Research priorities for dickcissels include investigating potential drivers of their low productivity and low adult survivorship (DeSante et al., 2015). Breeding females build bulky cup nests in dense, tall grasslands with scattered forbs; females typically place nests low (22–46 cm aboveground) in dense vegetation with overhead cover, but occasionally may build nests up to 4 m high in trees (Temple, 2020). Common grassland management strategies such as grazing, haying (mowing), and controlled burning prevent woody encroachment in the long term, but in the short term they simplify grassland structure, which may reduce dickcissels' habitat quality and ability to adjust to fluctuating climatic conditions (Zimmerman, 1992; Travis, 2003; Jarzyna et al., 2016). Since dickcissel nests are often attached loosely to supporting vegetation (Long et al., 1965; Gross, 1968), they are vulnerable to being knocked down during heavy precipitation events, which can cause loss of eggs and nestlings and reduce dickcissel breeding success (Zimmerman, 1966).

Obligate brood parasites, brown-headed cowbirds (*Molothrus ater*) lay their eggs in the nests of >220 avian host species rather than building their own nests (Lowther, 2020). In transferring the costs of raising their young to their hosts, cowbirds are entirely dependent on their hosts for their reproductive success (Smith et al., 2000; Croston and Hauber, 2010). Cowbirds remove eggs from nests they parasitize, reducing their hosts' nesting success, and are known to intensely parasitize dickcissels (Jensen and Cully, 2005; Temple, 2020). Studies have estimated that cowbird parasitism affects 48–90% of dickcissel nests (Basili et al., 1997; Temple, 2020) and significantly reduces dickcissel productivity (Zimmerman, 1983; Jensen and Cully, 2005). Before European settlement of the Great Plains, cowbirds followed migratory herds of American bison (*Bison bison*), and their impacts on their hosts during the breeding season were limited by their ephemeral presence at any given location. The extirpation of migratory bison and subsequent practice of confining sedentary livestock into fenced areas has transformed these patterns such that cowbirds now tend to concentrate in high densities where they remain throughout the breeding season. Their rates of parasitism on their hosts are correlated with their densities (Jensen and Cully, 2005). Birds with remarkable memories (Guigueno et al., 2014), female cowbirds may learn the whereabouts of most or all nests in their vicinity and parasitize them repeatedly. Previous research has suggested that cowbird parasitism may increase as dickcissel breeding densities decline, because the remaining hosts bear increasing pressure from the relatively higher proportion of cowbirds and their eggs (Zimmerman, 1982). The resulting pattern of inverse density dependence may further reduce dickcissel nest success and productivity (Temple, 2020). Few empirical studies to date have addressed whether or how weather influences cowbirds' interactions with their hosts (Colón et al., 2017; Buxton et al., 2018). Improving conservation strategies for dickcissels will include an increased understanding of the effects of weather and climate change on cowbird populations (DeSante et al., 2015). Dickcissels' particular vulnerability to cowbird parasitism also makes their populations valuable indicators of relationships with cowbirds and weather.

We took advantage of a rare opportunity to use 9 years of capture-recapture data collected systematically over an 18-year period to investigate whether dickcissel and cowbird abundance and productivity changed in relation to changes in weather in the eastern Great Plains. We quantified changes in dickcissel abundance and productivity in response to changes in precipitation and temperature as well as grassland management including grazing by cattle (*Bos taurus*) and bison, haying, and burning. We expected moderate levels of precipitation to benefit birds in this riparian ecosystem by increasing primary productivity and grassland structural complexity. However, we expected increasing precipitation to be associated with an increased number of heavy precipitation days and flooding that would in turn negatively affect dickcissels' abundance and productivity, including by reducing habitat and food resource availability. Cowbirds, on the other hand, are not known to decline in response to higher precipitation and therefore may be resilient to the negative effects it has on dickcissels and other grassland songbirds. Thus, we hypothesized that increases in precipitation would drive dickcissel declines and increase their vulnerability to cowbird parasitism.

MATERIALS AND METHODS

Study Area

We sampled birds at 17 sites in a 2430 ha private conservation area comprised of riparian upland prairies and wet meadows in Nebraska's Platte River Valley (**Figure 1**), where much of the surrounding land has been converted to industrial-scale agriculture, especially corn (*Zea mays*). In 1978, this fragment of the critically endangered North American Central and Southern Mixed Grasslands ecoregion was designated as protected habitat for the conservation of whooping cranes, sandhill cranes (*Antigone canadensis*), and other migratory birds. These grasslands comprise disturbance-dependent ecosystems (e.g., Glass et al., 2020). Ephemeral disturbances such as bison grazing, seasonal flooding, and wildfires historically structured this region, controlling woody encroachment and maintaining early successional vegetation (Williams, 1978; Anderson, 2006). The Crane Trust, a non-profit organization, now maintains these grasslands through managed disturbances including grazing, haying, and burning, which control woody encroachment. Cattle, brought in seasonally, were the sole grazers until 2015, when a semi-domesticated bison herd was introduced year-round to part of our study area (King et al., 2019). Cattle and bison grazing often overlap with the songbird breeding season, while haying

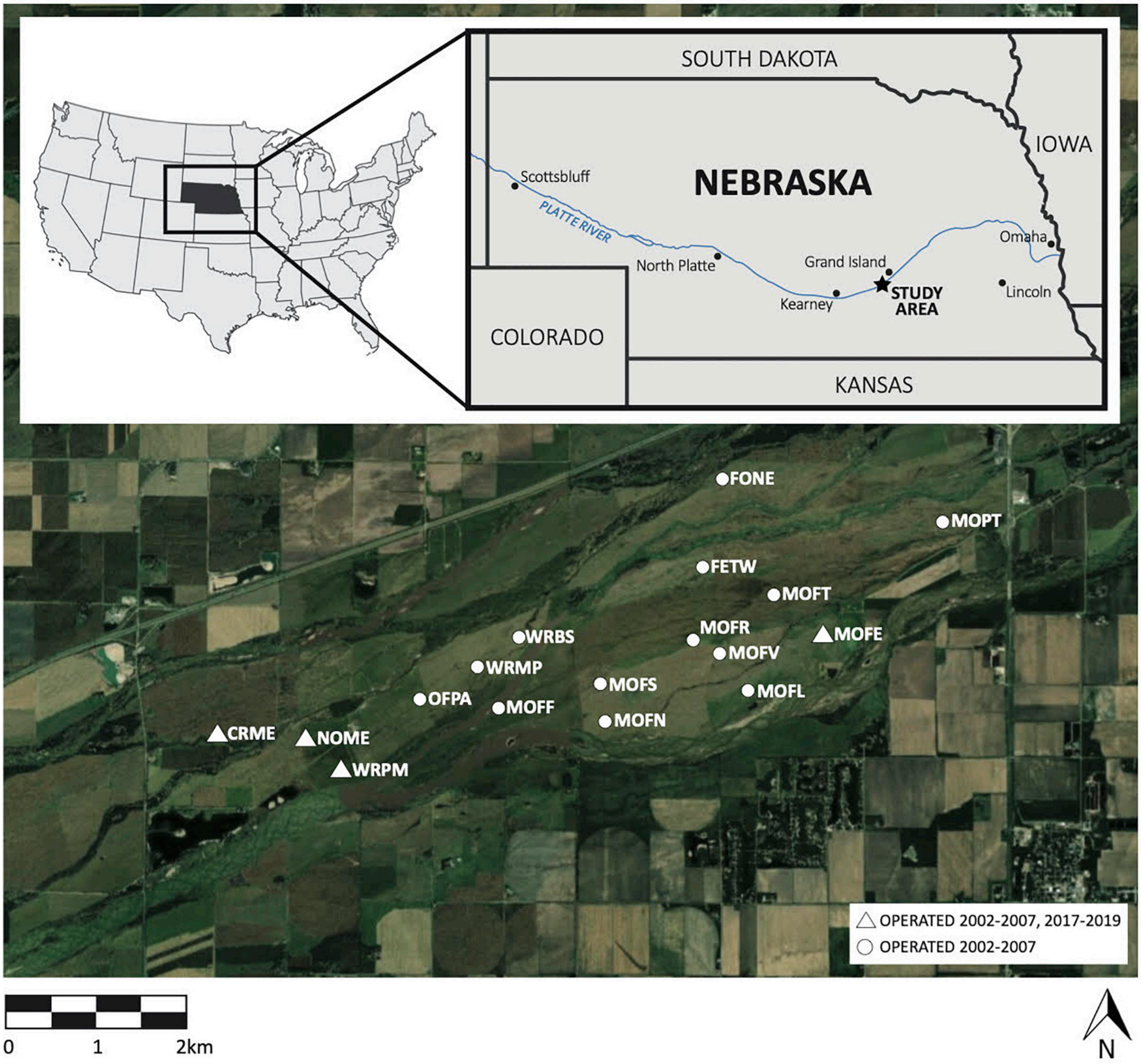

FIGURE 1 | Map of study area in North American Great Plains indicating bird sampling sites.

and burning typically take place during the non-breeding season, in the fall and spring, respectively.

Bird Sampling

We used protocols standardized by the MAPS program (DeSante and Kaschube, 2009; DeSante et al., 2017) to sample birds using constant-effort mist-netting at ∼20 ha stations (hereafter, sites) during the breeding season within the 80-day period from late May to early August. Between 2002 and 2007, we sampled birds at 17 sites, of which 3 were sampled for 6 consecutive years and 14 were sampled for periods ranging between 1 and 5 years. From 2017 to 2019, we replicated bird sampling at 4 sites used in 2002–2007 with different management histories for 3 consecutive years. Standardized in 1992, the MAPS program includes more than 1000 bird banding (ringing) stations (DeSante et al., 2015) that provide capture-recapture data from mist net sampling to assess avian population parameters and vital rates (DeSante et al., 2015; Foster et al., 2016; Saracco et al., 2016, 2019; Ahrestani et al., 2017; Glass et al., 2020). We identified captured birds to species and fitted them with a uniquely numbered aluminum band (ring) issued by the USGS Bird Banding Laboratory. We recorded demographic information and biometric measurements and then released birds at the site of capture (Pyle, 1997). We deployed 10–12 mist nets (12 × 3 m, 30 mm mesh) within a ∼8 ha area at each site (DeSante et al., 2017); we used 12 mist nets during the 2002–2007 data collection period and 10 mist nets during the 2017–2019 data collection period. Each sampling event consisted of a capture period of 6 h following sunrise (∼0600) and operated approximately once every 10 days. Effort was consistent for each sampling event, except when nets were occasionally closed during periods of high winds, heavy precipitation, or lightning storms, in which case we compensated by adding equal effort to a subsequent sampling occasion.

Capture-recapture sampling is a powerful tool for estimating animal abundance, and novel approaches to capture-recapture analyses are increasingly used to estimate abundance of open-population sizes from mark-recapture data on animals (Williams et al., 2002; Manly et al., 2003; Amstrup et al., 2005; Thomson et al., 2009; Gopalaswamy et al., 2012), expanding earlier uses of capture-recapture analyses that historically focused on estimating survival (Williams et al., 2002; Barker et al., 2004). Habitat types, seasons, and species' behavior and life histories may influence mist net capture rates (Remsen and Good, 1996; DeSante et al., 2015; Martin et al., 2017). Bearing in mind these caveats, appropriate use of mist net capture-recapture data allows us to standardize quantitative data on bird populations, including information on birds' sex, age, and biometrics, enabling the analysis of demographic parameters to generate insight into ecological processes.

We used MAPS protocols to collect data on songbirds during their breeding season. During this time, both male and female dickcissels make frequent, short flights (Temple, 2020) that facilitate their capture using mist nets (Remsen and Good, 1996). DeSante et al. (2015) analyzed dickcissel demographric data collected through the MAPS program between 1992 and 2006, a period that overlaps with our study period, providing a useful point of reference. Here, we follow DeSante et al. (2015) in quantifying avian productivity through our captures of post-fledging juvenile (hatch-year) birds. Productivity is influenced by the proportion of breeding adults, clutch size, nest survival, and nestling and juvenile survival after independence (DeSante et al., 2015) as well as cowbird parasitism (Temple, 2020). Previous research has indicated that dickcissel juveniles can disperse at least 600 m from nests within 10 days after fledging (Gross, 1921; Temple, 2020). We captured dickcissel juveniles still dependent on their mothers (i.e., adult females and juveniles were captured together) as well as dispersing juveniles that were independent.

Weather and Climate Parameters

We obtained weather data from the National Oceanic and Atmospheric Administration (NOAA, 2019) online database for South-Central Nebraska (station KGRI, 40.968°N, −98.340°W, Central Nebraska Regional Airport in Grand Island, Nebraska; approximately 21 km northeast of our research site). We created eight variables (**Table 1**) representing total precipitation (mm) and average temperature (°C) over different temporal scales. We used total precipitation, as provided in NOAA's database, as a measurement standard for modeling, as it accurately represents differences in monthly precipitation levels. We calculated total precipitation and average temperature for the main migratory songbird breeding season (June-July) of the current year, when precipitation and temperature directly affect breeding birds and their productivity. We also calculated total precipitation and average temperature for the previous non-breeding season (August-May), when precipitation and average temperature indirectly affect breeding birds and productivity through their effects on habitat, plant phenology, food resources, predators, and other factors. We also examined temperature and precipitation variables for June and July separately to determine whether conditions during either month of the breeding season affected dickcissels differently.

TABLE 1 | Weather parameters.

Variable	Type	Definition
August-May precipitation	Continuous	Total precipitation (mm) in the non-breeding season (August-May) of the preceding year
August-May temperature	Continuous	Average temperature (°C) in the non-breeding season (August-May) of the preceding year
June-July precipitation	Continuous	Total precipitation (mm) in the breeding season (June-July) of the current year
June-July temperature	Continuous	Average temperature (°C) in the breeding season (June-July) of the current year
June precipitation	Continuous	Total precipitation (mm) in June
June temperature	Continuous	Average temperature (°C) in June
July precipitation	Continuous	Total precipitation (mm) in July
July temperature	Continuous	Average temperature (°C) in July

TABLE 2 | Land management, habitat, and cowbird parameters.

Variable	Type	Definition
Native v restored habitat	Categorical	Remnant: grasslands that were never tilled for agriculture; restored: grasslands replanted after being previously used for agriculture
Historic flooding frequency	Categorical	No flooding (0), very rare flooding (1), rare flooding (2), occasional flooding (3), frequent flooding (4), very frequent flooding (5)
Months since grazing	Continuous	Months since the site was last grazed
Grazing intensity	Continuous	Grazing effort (AUM/ha) of the site at the time the sample was taken
Grazing history	Continuous	Average AUM/ha of the site for the past 5 years at the time the sample was taken
Months since haying	Continuous	Months since the site was last hayed
Months since burning	Continuous	Months since the site was last burned
Adult cowbirds	Continuous	Total number of adult cowbirds captured by site and year
Hatch-year cowbirds	Continuous	Total number of hatch-year cowbirds captured by site and year
Female cowbirds	Continuous	Total number of female cowbirds captured by site and year

Land Management and Habitat Parameters

We created seven habitat and land management parameters (**Table 2**). Three variables represent time (months) since managed disturbances (grazing, haying, and burning) at sampling sites. We set the maximum time since disturbance value for grazed, hayed, and burned pastures at 180 months

(15 years) because management actions that occurred earlier were unlikely to have a predictable effect on habitat structure (Collins, 2000). In addition, we created two management parameters (grazing intensity and grazing history) representing livestock (cattle or bison) stocking rate for grazed pastures in animal unit months per hectare (AUM/ha), where one AUM equals the forage requirement for one adult and calf pair for a 1-month period (Hamilton, 2007; Johnson et al., 2011). Grazing intensity is represented by AUM/ha at each study site at the time of data collection; a value of 0 represents sites that had no grazing during MAPS data sampling. Grazing history is represented by the average AUM/ha at each site for the current year plus the 4 years preceding data collection (Glass et al., 2020). In addition, we created a categorical variable to distinguish native remnant grasslands with no major disturbance history from restored grasslands on land previously used for row agriculture or planted with exotic grasses. We created another categorical variable representing historic flooding frequency by averaging flooding frequency of soil (none, very rare, rare, occasional, frequent, very frequent) within the sampling footprint as indicated by USDA soil maps. When this footprint included over three soil types, we averaged the top three values.

Statistical Analyses

We conducted all statistical analyses using R Studio version 3.6.2 (R Core Team, 2019). We used dickcissel capture data across all 17 sites, removing recaptures of individuals that occurred at the same site during the same year to avoid double-counting. In addition to quantifying dickcissel numbers, we used the same methods to quantify adult, juvenile, and female cowbirds in all sites and all years sampled. We corrected for effort by dividing the number of captures by the cumulative mist net-meter-hours for the given year. We divided the banding season into two halves for data analysis, in which the first half comprised adults arriving and establishing breeding territories and nests, and the second half comprised both adults and juvenile birds that had fledged from successful nests (Glass et al., 2020). The first half of the banding season included MAPS periods 3–6 (May 21-June 29), and the second half included MAPS periods 7–10 (June 30-August 8) (DeSante et al., 2017).

Pastures were often grazed for the first or second half of the summer, such that in some cases values for variables such as time (months) since grazing and current stocking rate changed for a given pasture within a banding season. We tested for correlations between climate and management parameters with a Spearman's correlation test to account for the non-normal distribution of parameters, using the package *psych* (Revelle, 2018). We used the uncorrelated variables ($r < |0.7|$; **Table 3**) to perform two independent generalized linear mixed models (GLMMS), one for adult and another for juvenile dickcissels. We log-transformed all of the continuous parameters prior to analysis for better convergence. After analyzing different possible combinations including linear, quadratic, and interaction terms, we used Akaike's Information Criterion (AIC) to select the models that best fit the data (**Table 4**). For analysis of adults, we used a

TABLE 3 | Correlation matrix of variables.

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1. Historic flooding frequency	1.00																	
2. Native v restored habitat	0.08	1.00																
3. Months since grazing	−0.19	0.18	1.00															
4. Grazing intensity	0.10	−0.02	−0.73	1.00														
5. Grazing history	0.12	−0.35	−0.78	0.42	1.00													
6. Months since haying	0.16	−0.22	−0.57	0.24	0.65	1.00												
7. Months since burning	−0.14	0.32	0.21	−0.20	−0.24	−0.09	1.00											
8. Adult cowbirds	0.05	−0.19	−0.17	0.14	0.20	0.22	−0.23	1.00										
9. Hatch-year cowbirds	0.11	−0.14	−0.22	0.08	0.28	0.25	−0.09	0.40	1.00									
10. Female cowbirds	0.07	−0.13	−0.12	0.11	0.13	0.14	−0.21	0.87	0.18	1.00								
11. August-May precipitation	0.12	−0.03	−0.33	0.23	0.22	0.03	−0.15	0.27	0.29	0.17	1.00							
12. August-May temperature	−0.06	−0.07	0.26	−0.24	−0.09	0.04	0.09	0.02	−0.08	0.07	−0.67	1.00						
13. June-July precipitation	0.07	0.00	−0.36	0.25	0.23	0.06	−0.17	0.29	0.23	0.23	0.63	−0.64	1.00					
14. June-July temperature	−0.04	−0.05	0.14	−0.20	−0.06	−0.04	0.09	−0.12	−0.03	−0.10	−0.23	0.67	−0.43	1.00				
15. June precipitation	0.06	−0.01	−0.15	0.07	0.12	−0.04	0.08	0.05	0.04	−0.02	0.61	−0.31	0.29	−0.08	1.00			
16. June temperature	−0.04	−0.02	0.10	−0.20	−0.07	−0.07	0.11	−0.18	−0.05	−0.16	−0.16	0.53	−0.33	0.96	−0.01	1.00		
17. July precipitation	0.03	0.03	−0.29	0.18	0.17	0.05	−0.11	0.20	0.14	0.19	0.21	−0.35	0.82	−0.37	−0.16	−0.32	1.00	
18. July temperature	−0.05	−0.06	0.27	−0.20	−0.13	−0.05	0.10	−0.23	−0.12	−0.20	−0.39	0.66	−0.84	0.73	−0.10	0.61	−0.78	1.00

Variables with correlations higher than |0.70| were not included in the same models.

TABLE 4 | AIC table for all models.

Model type	Model name	Description	Function	Formula	Family	AIC	ΔAIC
Dickcissel adult model	m	Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]	glmer	abundance ∼ period + mesic + land.use + graze.months + hay.months + burn.months + precip.aug.may + avg.temp.aug.may + precip.june.july + avg.temp.june.july + precip.june + burn.months * graze.months + (1|site), family = poisson, data = datsc	Poisson	9726.3	8304.7
Dickcissel adult model	m1	Model corrected for zero-inflation	glmmTMB	abundance ∼ period + mesic + land.use + graze.months + hay.months + burn.months + precip.aug.may + avg.temp.aug.may + precip.june.july + avg.temp.june.july + precip.june + burn.months * graze.months + (1|site), ziformula = ∼1, family = poisson, data = datsc	Poisson	4913.2	3491.6
Dickcissel adult model	m2	Negative binomial model corrected for zero-inflation	glmmTMB	abundance ∼ mesic + period + land.use + graze.months + hay.months + burn.months + precip.aug.may + avg.temp.june.july + precip.june + (1|site), ziformula = ∼1, family = nbinom2, data = datsc	Negative binomial	1419.5	2.1
Dickcissel adult model	m3	Negative binomial model corrected for zero-inflation with two quadratic effects	glmmTMB	abundance ∼ mesic + period + land.use + graze.months + hay.months + burn.months + precip.aug.may + avg.temp.june.july + I(avg.temp.june.july^2) + I(precip.june^2) + precip.june + (1|site), ziformula = ∼1, family = nbinom2, data = datsc	Negative binomial	1421.6	0
Dickcissel hatch-year model	m	Binomial model with only linear effects	glmmTMB	HY ∼ graze.months + land.use + avg.temp.june.july + precip.june.july + (1|site), dispformula = ∼0, family = binomial, data = datsc	Binomial	230.7	
Cowbird adult model	m	Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]	glmer	abundance ∼ period + mesic + land.use + graze.months + hay.months + burn.months + precip.aug.may + avg.temp.aug.may + precip.june.july + avg.temp.june.july + precip.june + burn.months * graze.months + (1|site), family = poisson, data = dsc	Poisson	5069.1	3943.7
Cowbird adult model	m1	Model corrected for zero-inflation	glmmTMB	abundance ∼ period + mesic + land.use + graze.months + hay.months + burn.months + precip.aug.may + avg.temp.aug.may + precip.june.july + avg.temp.june.july + precip.june + burn.months * graze.months + (1|site), ziformula = ∼1, family = poisson, data = dsc	Poisson	2573.8	1448.4
Cowbird adult model	m2	Negative binomial model corrected for zero-inflation	glmmTMB	abundance ∼ mesic + period + land.use + graze.months + hay.months + burn.months + precip.aug.may + avg.temp.june.july + precip.june + (1|site), ziformula = ∼1, family = nbinom2, data = datsc	Negative binomial	1136.7	11.3
Cowbird adult model	m3	Negative binomial model corrected for zero-inflation with two quadratic effects	glmmTMB	abundance ∼ mesic + period + land.use + graze.months + hay.months + burn.months + precip.aug.may + avg.temp.june.july + I(avg.temp.june.july^2) + I(precip.june^2) + precip.june + (1|site), ziformula = ∼1, family = nbinom2, data = datsc	Negative binomial	1125.4	0
Cowbird juvenile model	m	Binomial model with only linear effects	glmmTMB	HY ∼ graze.months + land.use + avg.temp.june.july + precip.june.july + (1|site), dispformula = ∼0, family = binomial, data = datsc	Binomial	414.5	

“” Represents an interaction between two variables.*

negative binomial distribution to account for overdispersion of the data using the package *glmmTMB* (Brooks et al., 2017). The final model includes both linear and quadratic terms for temperature and precipitation as fixed factors, and site as a random factor to account for non-independent observations within each site. We also used the package *glmmTMB* to run models for juvenile dickcissels after we converted these data into a binomial response with a binomial distribution.

We modeled annual variation in captured dickcissels and cowbirds using GLMMs. For each species, we developed two models. The first model included the number of adults captured, an index of adult abundance (hereafter, abundance) as a response variable. The second model included whether a captured bird was a hatch-year bird (hereafter, productivity) as a response variable (DeSante et al., 2015; Foster et al., 2016; Glass et al., 2020). We created a binomial index to quantify productivity, assigning juvenile birds a value of 1 and adults a value of 0. Lastly, we ran a GLMM with adult cowbird abundance as a response variable and a GLMM with cowbird productivity as a response variable, using the same methods described above for dickcissel abundance and productivity, respectively.

We also ran a principal component analysis (PCA) to create a set of uncorrelated climate and management parameters. From the 10 original variables introduced by the PCA, we selected the first three principal components, which together explained 64.5% of the total variation. We performed the same analyses as above with the principal components and the three categorical variables with site as a random factor to check for consistency in our results. As our results were consistent with both approaches, we modeled the uncorrelated variables independently to allow us to interpret each variable using non-linear effects not shown by the PCA.

RESULTS

Between 2002 and 2019, we captured a total of 737 dickcissels (**Tables 5**, **6**), excluding recaptures from the same year and site. The number of adult dickcissels captured and banded per year ranged from 12 from four active sites in 2018 to 186 from 12 active sites in 2006 (mean = 78.3 ± 18.3 SE). Of adult dickcissels captured, 76% (*n* = 528) were male and 24% (*n* = 165) were female (the sex of 12 adult dickcissels was not recorded). We recaptured 50 adult dickcissels. Of same-year recaptures, 93% were at the same site as their initial capture and the remainder at adjacent sites within <10 km. Of subsequent-year recaptures, 70% were at the same site as their initial capture and the remainder at sites within <10 km. Juveniles (hatch-year birds) made up 4% of total dickcissel captures, which was the equivalent of one juvenile for every five adult female dickcissels. Juvenile numbers per year ranged from 0 in 2002, 2004, 2005, and 2019 to 17 in 2007 (mean = 3.6 ± 2.0 SE). We captured half of all dickcissel juveniles at a single site (MOFE) and over half in a single year (2007; **Table 6**).

We found a weak positive correlation between numbers of dickcissels and cowbirds, for both abundance (Spearman's rank correlation test: rho = 0.237, $p = 0.004$) and productivity (rho = 0.294, $p = 0.0002$). Between 2002 and 2019, we captured a total of 442 adult cowbirds (**Table 7**), excluding recaptures from the same year and site. The number of adult cowbirds captured and banded per year ranged from 0 in 2002 to 132 in 2005 (mean = 49.1 ± 17.0 SE). Of adult cowbirds we banded, 49% (*n* = 206) were female and 51% (*n* = 199) were male (the sex of 37 cowbirds was not recorded). Juveniles represented 14% of our total cowbird captures (**Table 8**), which was the equivalent of one juvenile for every three adult female cowbirds. For both species, we made more captures of adult birds during the first half of the breeding season, when new arrivals were establishing territories and breeding (dickcissels: $Z = 5.09$, $p = 3.54e{-}07$; cowbirds: $Z = 7.93$, $p = 2.21e{-}15$; **Table 9**). This pattern in part

TABLE 5 | Adult dickcissel captures by site and year.

Site	2002	2003	2004	2005	2006	2007	2017	2018	2019	Total
CRME	–	9	8	–	–	–	6	4	4	31
FETW	–	–	–	11	8	9	–	–	–	28
FONE	–	19	18	16	37	22	–	–	–	112
MOFE	44	23	20	2	13	35	0	4	4	145
MOFF	10	–	7	2	8	3	–	–	–	30
MOFL	–	8	–	–	–	–	–	–	–	8
MOFN	10	–	3	4	14	0	–	–	–	31
MOFR	–	9	–	8	18	6	–	–	–	41
MOFS	2	–	–	–	–	–	–	–	–	2
MOFT	9	14	1	19	22	2	–	–	–	67
MOFV	10	–	–	3	4	–	–	–	–	17
MOPT	–	–	–	7	33	11	–	–	–	51
NOME	–	6	13	0	3	0	16	1	8	47
OFPA	–	1	2	–	–	10	–	–	–	13
WRBS	18	10	1	–	9	–	–	–	–	38
WRMP	–	–	–	7	–	–	–	–	–	7
WRPM	4	4	0	2	17	0	4	3	3	37
Total	107	103	73	81	186	98	26	12	19	705

Numbers represent abundance values used in dickcissel analyses. All birds are included except those recaptured in the same site during the same year. Dashes represent years in which a site was operated.

TABLE 6 | Hatch-year dickcissel captures by site and year.

Site	2002	2003	2004	2005	2006	2007	2017	2018	2019	Total
CRME	–	0	0	–	–	–	0	0	0	0
FETW	–	–	–	0	0	0	–	–	–	0
FONE	–	0	0	0	4	5	–	–	–	9
MOFE	0	0	0	0	2	12	1	1	0	16
MOFF	0	–	0	0	0	0	–	–	–	0
MOFL	–	0	–	–	–	–	–	–	–	0
MOFN	0	–	0	0	0	0	–	–	–	0
MOFR	–	0	–	0	0	0	–	–	–	0
MOFS	0	–	–	–	–	–	–	–	–	0
MOFT	0	0	0	0	1	0	–	–	–	1
MOFV	0	–	–	0	0	–	–	–	–	0
MOPT	–	–	–	0	4	0	–	–	–	4
NOME	–	0	0	0	0	0	0	1	0	1
OFPA	–	0	0	–	–	0	–	–	–	0
WRBS	0	1	0	–	0	–	–	–	–	1
WRMP	–	–	–	0	–	–	–	–	–	0
WRPM	0	0	0	0	0	0	0	0	0	0
Total	0	1	0	0	11	17	1	2	0	32

Numbers represent number of hatch-year dickcissels used in productivity analyses. All birds are included except those recaptured in the same site during the same year. Dashes represent years in which a site was not operated.

TABLE 7 | Adult cowbird captures by site and year.

Site	2002	2003	2004	2005	2006	2007	2017	2018	2019	Total
CRME	–	0	3	–	–	–	1	1	0	5
FETW	–	–	–	15	7	6	–	–	–	28
FONE	–	4	8	9	5	12	–	–	–	38
MOFE	0	9	7	2	2	26	11	3	0	60
MOFF	0	–	7	12	6	19	–	–	–	44
MOFL	–	1	–	–	–	–	–	–	–	1
MOFN	0	–	6	8	8	3	–	–	–	25
MOFR	–	1	–	17	13	8	–	–	–	39
MOFS	0	–	–	–	–	–	–	–	–	0
MOFT	0	7	8	21	9	15	–	–	–	60
MOFV	0	–	–	5	3	–	–	–	–	8
MOPT	–	–	–	8	5	9	–	–	–	22
NOME	–	1	8	13	2	7	0	4	1	36
OFPA	–	3	7	–	–	9	–	–	–	19
WRBS	0	2	2	–	8	–	–	–	–	12
WRMP	–	–	–	11	–	–	–	–	–	11
WRPM	0	0	6	11	9	5	3	0	0	34
Total	0	28	62	132	77	119	15	8	1	442

Numbers represent abundance values used in brown-headed cowbird analyses. All birds are included except those recaptured in the same site during the same year. Dashes represent years in which a site was not operated.

reflects trap-shyness of birds that avoided nets after being trapped and banded although they remained on site (Simons et al., 2015).

Dickcissel Responses to Weather, Land Management, and Habitat Parameters

Dickcissel abundance was negatively correlated with June precipitation (Z = 2.01, p = 0.04; **Table 9** and **Figure 2**). Of the parameters we tested, June precipitation was the only significant predictor of dickcissel abundance, although we found near-significant positive correlations with both time since grazing (graze months: p = 0.061) and time since haying (hay months: p = 0.054), indicating that dickcissel abundance may increase with increasing time since grazing and haying for at least 15 years (>180 months) in this ecosystem. Dickcissel productivity was positively correlated with June-July precipitation (Z = 4.156, p = 3.23e-05), June-July temperature (Z = 2.622, p = 0.009), and months since grazing (Z = 2.236, p = 0.03; **Table 10** and **Figure 3**).

TABLE 8 | Juvenile cowbird captures by site and year.

Site	2002	2003	2004	2005	2006	2007	2017	2018	2019	Total
CRME	–	0	0	–	–	–	0	0	0	0
FETW	–	–	–	2	0	4	–	–	–	6
FONE	–	0	0	2	1	5	–	–	–	8
MOFE	0	0	1	0	0	9	2	1	0	13
MOFF	0	–	0	3	1	7	–	–	–	11
MOFL	–	0	–	–	–	–	–	–	–	0
MOFN	0	–	1	2	0	0	–	–	–	3
MOFR	–	0	–	1	3	4	–	–	–	8
MOFS	0	–	–	–	–	–	–	–	–	0
MOFT	0	1	1	3	2	4	–	–	–	11
MOFV	0	–	–	0	2	–	–	–	–	2
MOPT	–	–	–	2	1	2	–	–	–	5
NOME	–	0	0	0	0	0	0	0	1	1
OFPA	–	0	1	–	–	0	–	–	–	1
WRBS	0	0	0	–	0	–	–	–	–	0
WRMP	–	–	–	0	–	–	–	–	–	0
WRPM	0	1	0	0	0	1	0	0	0	2
Total	0	2	4	15	10	36	2	1	1	71

Numbers represent number of hatch-year brown-headed cowbirds used in productivity analyses. All birds are included except those recaptured in the same site during the same year. Dashes represent years in which a site was not operated.

TABLE 9 | Adult bird model results.

Species	Variable	Estimate	Standard Error	*Z* Value	*p* value[1]
Dickcissel	Intercept	4.294	0.204	21.008	<0.001***
	Early v late summer	0.686	0.135	5.092	<0.001***
	Native v restored habitat	−0.291	0.264	−1.099	0.272
	Historic flooding frequency	−0.097	0.108	−0.898	0.369
	June precipitation	−0.291	0.145	−2.008	0.045*
	June precipitation (quadratic)	0.133	0.170	0.781	0.435
	August-May precipitation	−0.096	0.109	−0.879	0.379
	June-July temperature	0.031	0.120	0.254	0.799
	June-July temperature (quadratic)	−0.242	0.186	−1.305	0.192
	Months since grazing	−0.259	0.138	−1.872	0.061·
	Months since haying	−0.275	0.143	−1.931	0.054·
	Months since burning	−0.006	0.095	−0.064	0.949
Cowbird	Intercept	3.212	0.225	14.267	<0.001***
	Early v late summer	1.069	0.135	7.929	<0.001***
	Native v restored habitat	−0.338	0.159	−2.133	0.033*
	Historic flooding frequency	0.030	0.060	0.503	0.615
	June precipitation	−0.443	0.131	−3.383	0.001***
	June precipitation (quadratic)	0.654	0.164	3.987	<0.001***
	August-May precipitation	0.301	0.147	2.047	0.041*
	June-July temperature	0.392	0.259	1.509	0.131
	June-July temperature (quadratic)	−0.119	0.240	−0.496	0.620
	Months since grazing	0.119	0.121	0.984	0.325
	Months since haying	0.138	0.121	1.147	0.251
	Months since burning	−0.025	0.117	−0.212	0.832

*Decimal values are rounded to the thousandths place value. [1]Asterisks and periods represent significance levels ("***" 0.001, "*" 0.05, "·" 0.1).*

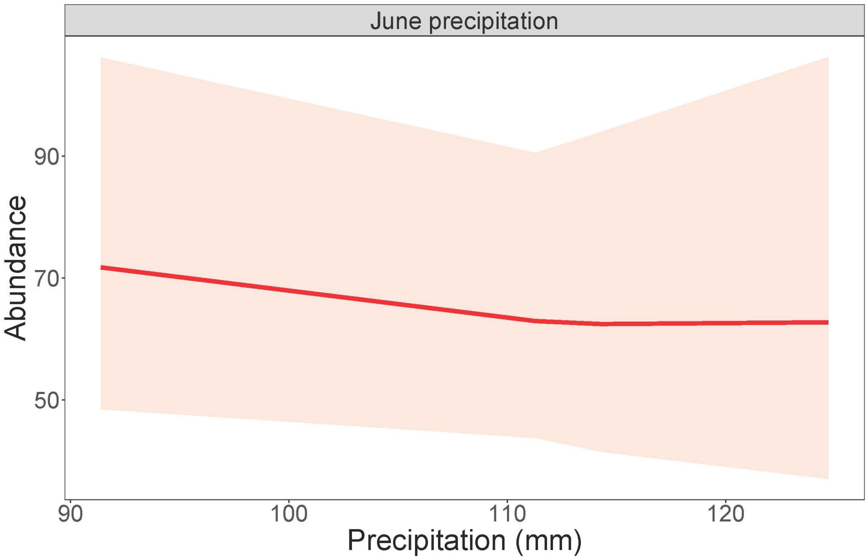

FIGURE 2 | Dickcissel abundance in response to June precipitation. Total June precipitation plotted against numbers of individual adult birds, within a 95% confidence interval.

TABLE 10 | Juvenile index bird model results.

Species	Variable	Estimate	Standard Error	*Z* Value	*p* value[1]
Dickcissel	Intercept	−3.690	0.494	−7.477	<0.001***
	Native v restored habitat	−21.020	9661.479	−0.002	0.998
	June-July precipitation	1.551	0.373	4.156	<0.001***
	June-July temperature	1.055	0.402	2.622	0.009**
	Months since grazing	0.747	0.334	2.236	0.025*
Brown-headed cowbird	Intercept	−1.881	0.188	−9.986	<0.001***
	June-July precipitation	0.384	0.136	2.833	0.005**

Decimal values are rounded to the thousandths place value. [1] *Asterisks and periods represent significance levels ("***" 0.001, "**" 0.01, "*" 0.05).*

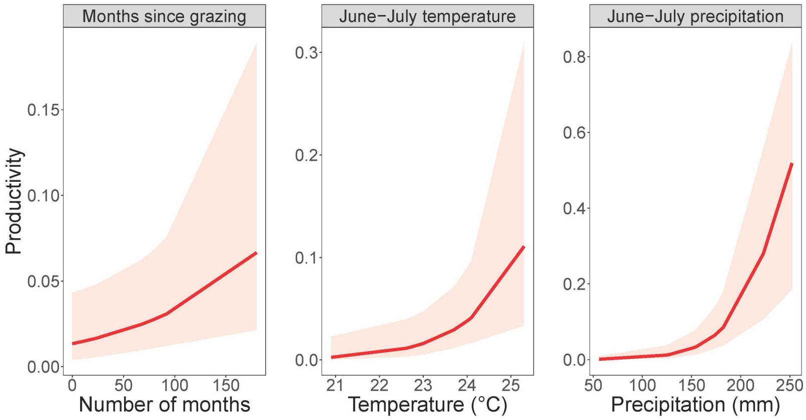

FIGURE 3 | Dickcissel productivity in response to grazing and summer precipitation and temperature. Plots depict (from left to right) months since grazing, mean June-July temperature, and total June-July precipitation plotted against dickcissel productivity, or the probability of encountering a juvenile bird, within 95% confidence intervals.

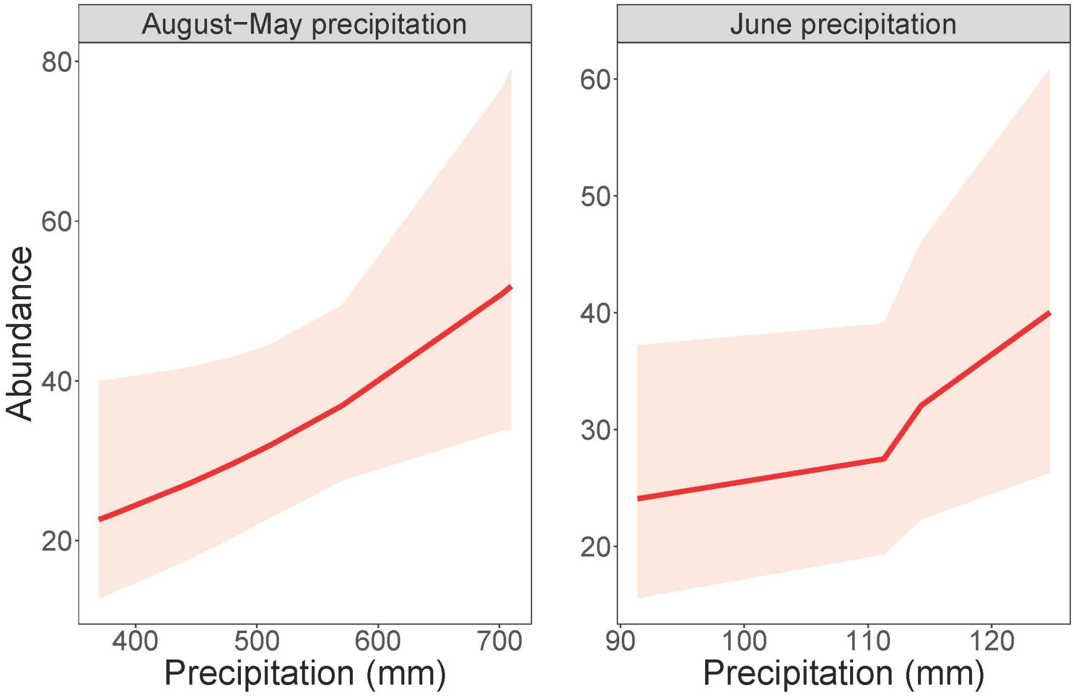

FIGURE 4 | Cowbird abundance in response to precipitation during both the non-breeding season (August-May) and June. Total August-May precipitation (left) and total June precipitation (right) plotted against numbers of individual adult birds, within 95% confidence intervals.

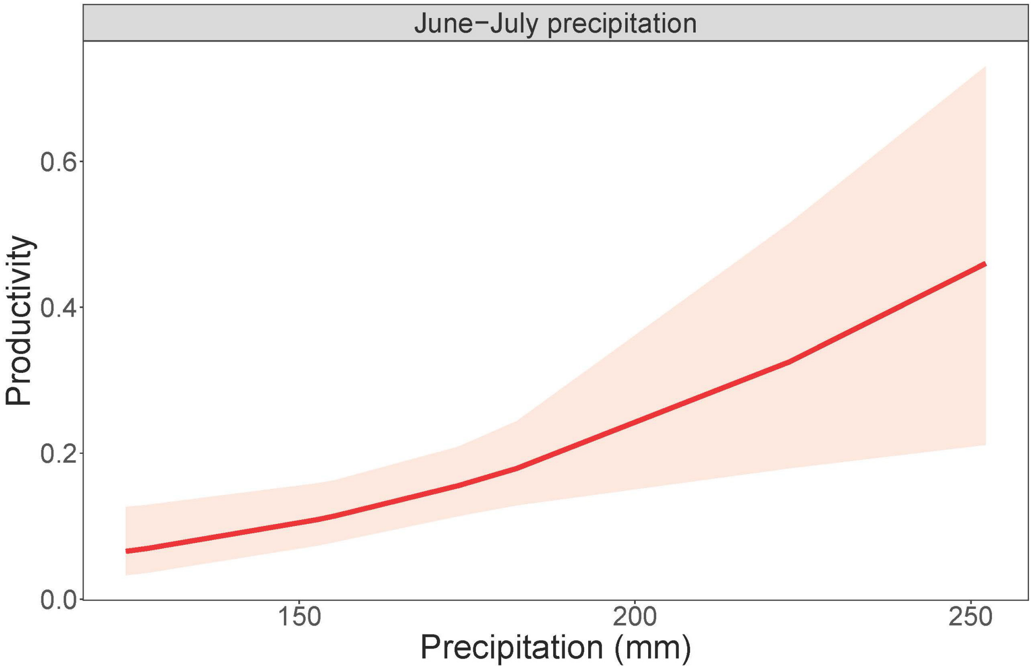

FIGURE 5 | Cowbird productivity in response to summer precipitation. Total June-July precipitation plotted against cowbird productivity, or the probability of encountering a juvenile bird, within a 95% confidence interval.

Cowbird Responses to Weather, Land Management, and Habitat Parameters

Cowbird abundance exhibited a quadratic positive relationship with June precipitation (Z = 3.99, p = 6.70e-05; **Table 9** and **Figure 4**). In addition, cowbird abundance had a positive relationship with non-breeding season (August-May) precipitation (Z = 2.05, p = 0.04). We captured more cowbirds in remnant prairie fragments compared to grasslands restored after they were planted with invasive grasses or agricultural crops (Z = −2.13, p = 0.03, **Table 9**). Cowbird productivity was positively correlated with June-July precipitation (Z = 2.833, p = 0.01; **Table 10** and **Figure 5**).

DISCUSSION

Dickcissel Relationships With Precipitation and Grassland Management

Dickcissel abundance declined with increasing June precipitation, corroborating previous research showing that dickcissel and other breeding songbird densities in this area decreased with increasing levels of moisture (Kim et al., 2008). These findings contrast with previous research elsewhere in the Great Plains testing the "climate bottleneck hypothesis" that found that grassland breeding bird abundance did not significantly change in response to changes in precipitation (Wiens, 1973; Zimmerman, 1992), with the important caveat that our study areas differed in their proximity to riparian corridors and therefore flooding potential. Our findings also contrast with a pattern of increasing bird abundance with increasing precipitation for wetland bird species elsewhere in the Great Plains (Mantyka-Pringle et al., 2019). Dickcissel abundance decreased with increased precipitation during the breeding season but not the non-breeding season (when they are away), implying that negative effects of increased precipitation on dickcissels stem from direct effects during the breeding season, such as emigration due to heavy precipitation and related extreme events including flooding and summer hailstorms. High precipitation and extreme precipitation events may also cause direct mortality of adults and nestlings as well as nest failures, and changes in precipitation may influence exposure to predators (e.g., Takagi, 2001; Mattsson and Cooper, 2009; Robinson et al., 2017; Godwin et al., 2019).

Dickcissels showed high site fidelity, with 70–93% of recaptures occurring at the same site as that of initial capture. This is consistent with findings from other mark-recapture studies demonstrating dickcissels' fidelity to breeding sites in successive years in their core breeding range (Zimmerman and Finck, 1989; Temple, 2020). The male-biased sex ratio (3 males: 1 female) we found is consistent with male-biased sex ratios detected in other studies of this species on both its breeding and wintering grounds (ffrench, 1967; Fretwell and Calver, 1969; Fretwell, 1977; Basili and Temple, 1999). Fretwell (1977) hypothesized that the conversion of natural grasslands to crops has resulted in a novel winter food supply with larger (crop) seeds rather than smaller (native grass) seeds that in turn favors higher survival of larger (male) birds whose bills are better equipped to crush the larger seeds. Previous research has suggested that male-biased sex ratios may be more pronounced in dickcissel populations in the northern portions of their breeding range, such as in our study area, and have negative implications for dickcissels' breeding success, particularly given that dickcissels evolved polygyny, in which males typically mate with multiple females (Zimmerman, 1966; Fretwell, 1977; Temple, 2020). Female densities were low in our study area, and low female densities are associated with low productivity, underlining their vulnerability to declines (Fretwell and Calver, 1969; Fretwell, 1977; Hixon and Johnson, 2009).

Dickcissel abundance showed near-significant positive correlations with both time since grazing and time since haying, increasing with time since disturbance for at least 180 months (15 years), the maximum length of post-disturbance grassland regeneration considered in this study. Dickcissels' preference for breeding sites with tall, dense grasses and scattered forbs, and their positive responses to management that maintains these conditions, are well-established (e.g., Dechant et al., 2002). Dickcissels and other grassland birds consume some arthropods, such as Hymenoptera, that may be more abundant in ungrazed areas since cattle may disturb or trample them (Hoernemann et al., 2001). Dickcissels also consume Orthopteran species (Gross, 1921; Kobal, 1990), which some studies have shown to decline as a result of grazing (Capinera and Sechrist, 1982; Fielding and Brusven, 1995; but see Horn and Dowell, 1974; Hoernemann et al., 2001). Other research has found negative relationships between dickcissel abundance and recent grassland disturbance (Winter, 1998). Multi-year periods between haying events allow the development of dense vegetation including grasses, forbs, and woody plants that provide food, shelter, and nest sites (Temple, 2020). While hayed grasslands may provide nesting habitat for dickcissels and other grassland nesting birds when haying occurs after the breeding season, they create ecological traps when haying occurs during the breeding season because haying destroys nests, killing nestlings and reducing habitat quality (Luscier and Thompson, 2009; Prestby and Anich, 2013). Haying also reduces food availability for dickcissels and other insectivorous birds, as Orthopterans, ants, millipedes, and other invertebrates are sensitive to the mechanical disturbance associated with haying (Evans, 1988; Hoernemann et al., 2001; Jonas et al., 2002; Humbert et al., 2009). Arthropod declines resulting from haying may cause dickcissels and other birds to leave for more suitable habitat (James and Neal, 1986; Zalik and Strong, 2008). Dickcissels and other grassland obligate species may benefit from access to grasslands featuring a mosaic of successional times since disturbance (e.g., Hamilton, 2007; Murray et al., 2016).

While land management is clearly important for dickcissel and other grassland bird conservation (Dechant et al., 2002; Temple, 2020), our findings show that precipitation exerts a stronger influence than management in this riparian ecosystem. Broader-scale climate effects can also influence dickcissels' settlement decisions (Jensen and Cully, 2005), for example if dickcissels concentrate in the southern part of their breeding range in wetter years and in the northern part of their range in drier years or vice versa. Climate change may thus influence bird species on a broader scale, as geographic shifts in climate envelope may sometimes outweigh effects of local land management (Barbet-Massin et al., 2012; Sohl, 2014; Mantyka-Pringle et al., 2019). Other factors not captured in this study may also influence breeding bird populations, such as carry-over effects, which recent students have suggested are widespread and important in many bird species (Harrison et al., 2011; O'Connor et al., 2014) and can be sex- and age-specific (Saino et al., 2017; López-Calderón et al., 2019). Wintering area precipitation, habitat, and resources may thus influence arrival times and productivity of migratory songbirds on their breeding grounds (e.g., Marra et al., 1998; Robb et al., 2008; McKinnon et al., 2015; Akresh et al., 2019; López-Calderón et al., 2019). For example, Eurasian blue tits (*Cyanistes caeruleus*) with higher winter food availability laid eggs earlier and exhibited higher chick fledging rates (Robb et al., 2008). Previous research has suggested that winter mortality of dickcissels may have driven their past population declines and/or their male-biased sex ratios (Fretwell, 1973; Basili and Temple, 1999). Dickcissel breeding densities may also be negatively correlated with adult survival, which tends to be substantially lower than that of other songbird species comparable in size (DeSante et al., 2015). Whether winter-driven mortality and/or carry-over effects currently limit dickcissel populations is an important question for future research (Temple, 2020).

Cowbird Relationships With Precipitation and Dickcissels

While dickcissels declined during years with higher precipitation, cowbird abundance increased. Because increasing precipitation contributes to declining dickcissel abundance and increasing cowbird abundance simultaneously, dickcissels may be exposed to greater parasitism pressure from larger proportions of cowbirds in the same breeding area. In addition, we captured higher numbers of cowbirds in native remnant grasslands compared to restored grasslands, while dickcissel numbers did not appear to differ between remnant and restored grasslands. This finding suggests that cowbird parasitism on dickcissels and other hosts may be more frequent and intense in native remnant grasslands, driving ecological traps if dickcissels and other hosts are attracted to habitats that function as population sinks (Hale and Swearer, 2016). Cowbird parasitism intensity varies considerably at landscape scales (Jensen and Cully, 2005). Previous research found that cowbird densities mirrored dickcissel densities, either due to cowbirds tracking dickcissels, similar habitat, and/or similar foraging preferences (Kim et al., 2008). Several studies have suggested that cowbird parasitism may contribute to inverse density dependence in species including dickcissels (Zimmerman, 1966; Fretwell, 1977; Temple, 2020) and can therefore accelerate declines of small and fragmented host populations (Courchamp et al., 1999; Lowther, 2020), such as in our study area.

Dickcissels sustain high rates of cowbird parasitism through much or all of their breeding range, both in terms of the number of dickcissel nests affected and the number of cowbird eggs placed in each nest. Multiple studies have shown that dickcissels are the most parasitized grassland breeding bird species (Patterson and Best, 1996; Rivers et al., 2010) and that dickcissel productivity is reduced in parasitized nests (Fretwell, 1977; Jensen and Cully, 2005; Temple, 2020). Whereas only June precipitation influenced dickcissel abundance, cowbird abundance increased with both June and non-breeding season precipitation, suggesting that cowbirds benefit indirectly from higher precipitation and its relationship with greater plant growth and habitat complexity, which in turn can provide for food birds in the form of seeds and arthropods. When more frequent and heavy June rain may flood dickcissel habitat in this riparian area and in extreme cases (such as summer hail, which occurred multiple times during the study period), knock down nests, causing dickcissels to emigrate, cowbirds are not constrained by breeding territories or particular nests in the same way. In addition to their relationships with dickcissels, cowbird densities are locally related to other host densities, including their fellow Icterids, red-winged blackbirds (*Agelaius phoeniceus*) and bobolinks (*Dolichonyx oryzivorus*). Thus, in years with higher precipitation they have the flexibility to switch to these and other avian hosts that may be more tolerant of high June precipitation than dickcissels. For both dickcissels and cowbirds, precipitation was the only significant predictor of abundance of the weather and management factors we tested, highlighting the importance of precipitation in mediating interactions between cowbirds, dickcissels, and other hosts on their breeding grounds.

Dickcissel and Cowbird Productivity and Implications for Population Trends

Dickcissel productivity was positively correlated with breeding season precipitation, temperature, and time since grazing. Higher precipitation may benefit dickcissel productivity and juvenile survival by promoting greater grassland productivity (Rotenberry and Wiens, 1991; Chase et al., 2005), structural complexity, and food abundance (Rotenberry and Wiens, 1991; Skagen and Yackel Adams, 2012). Like that of dickcissels, cowbird productivity increased with increased June-July precipitation, meaning that increasing numbers of cowbirds were raised by hosts including dickcissels. In other riparian ecosystems, higher avian productivity has also been found to be positively correlated with precipitation, such as in Louisiana waterthrush (*Parkesia motacilla*; Mattsson and Cooper, 2009) and Mississippi kites (*Ictinia mississippiensis*; Welch-Acosta et al., 2019). By contrast, in other ecosystems, higher precipitation resulted in higher losses of nestlings to predators in bull-headed shrikes (*Lanius bucephalus*) (Takagi, 2001) and lower productivity in peregrine falcons (*Falco peregrinus*; Robinson et al., 2017) and tree swallows (*Tachycineta bicolor*; Godwin et al., 2019).

Dickcissel productivity was also positively correlated with breeding season temperature. The relatively high temperatures (36–40.5°C) at which optimal songbird egg development occurs may help explain this (DuRant et al., 2013). This finding contrasts with studies of other avian species in hotter climates in which higher temperatures (33–39°C, in contrast with July temperatures of 20–31°C in our study area) were associated with lower productivity (e.g., van de Ven et al., 2020). In addition, the positive correlation we found between dickcissel productivity and time since grazing may derive in part from greater predation risks to juvenile dickcissels in recently disturbed fields due to lack of vegetative cover (Bollinger et al., 1990; Suedkamp Wells et al., 2007). Past research has found that predation may cause half of dickcissel nest failures (Zimmerman, 1966; Fretwell, 1977). Nest predators include snakes and ground squirrels (*Spermophilus sp.*; Temple, 2020), both of which were present at our sites. Longer periods of time since grazing may also favor productivity in that grasslands with taller vegetation provide birds and their nests and nestlings with shade and shelter that have a buffering effect against higher, more variable temperatures (Dechant et al., 2002; Geiger et al., 2009; Villegas et al., 2010; Jarzyna et al., 2016).

In dickcissel populations with male-biased sex ratios, such as in our study system, low female densities may drive low productivity (Fretwell, 1977). Although the extremely low ratio of juvenile to adult dickcissels we found likely underestimates dickcissels' true productivity, DeSante et al. (2015) likewise found extremely low dickcissel productivity, averaging 80–90% lower than that of most other North American songbirds. Although dickcissel breeding densities peak in their core breeding range, male territoriality appears to limit them (Fretwell, 1977; Temple, 2020). Studies elsewhere have suggested that dickcissel productivity declines at lower densities, possibly due to higher cowbird parasitism levels (Zimmerman, 1966; Fretwell, 1977; Temple, 2020). However, here we found that although dickcissel adult abundance declined with increasing precipitation, their productivity increased. This finding corroborates other research suggesting that dickcissel populations may be regulated through density dependence (DeSante et al., 2015; Temple, 2020), for example if reduced competition for resources among fewer breeding adults may enable higher population growth due to higher survival rates of their young (Hixon and Johnson, 2009). As losses of adults are partially offset by higher numbers of juveniles, this response may be mitigating a significant decline of dickcissels in this area as precipitation has increased over time. However, dickcissels' low productivity overall may not be sufficient to counteract the declining trend in their abundance, as survival appears to be a stronger driver of population change than productivity in dickcissels (DeSante et al., 2015). Moreover, our findings suggest that cowbird abundance and parasitism rates may increase in the future wetter conditions predicted by climate change models for this region.

CONCLUSION AND FUTURE DIRECTIONS

Our findings highlight dickcissels' vulnerability to population declines due to increasing precipitation associated with climate change in this ecosystem, together with increasing cowbird abundance and parasitism that may further reduce dickcissel productivity. Precipitation has significantly increased in frequency and volume in the northeastern Great Plains, including our study area, in recent years (Wuebbles et al., 2014), and levels of precipitation are predicted to continue increasing in the coming decades (USGCRP, 2018). Our research reveals significant changes in avian population parameters related to changing weather and grassland management. Identifying the mechanisms driving these patterns will require additional research. How cowbird parasitism affects dickcissels and other breeding birds in relation to climate change merits particular attention (Lowther, 2020), given cowbirds' potential to reduce their hosts' productivity and contribute to population declines, especially in small and fragmented host populations common in temperate grasslands. Adaptive management for conservation (e.g., Dechant et al., 2002) that incorporates habitat heterogeneity remains essential to conserve dickcissels and other grassland specialists. In turn, targeted research to understand how grassland birds are responding to climate change and predict the consequences for their future populations is crucial to inform adaptive management strategies that mitigate the ongoing declines of grassland birds.

Understanding the interactions between cowbirds, dickcissels, and other host species, and how shifting weather patterns mediate these interactions, is an important consideration for grassland management and bird conservation under climate change. Future studies focused on dickcissels' and other species' responses to climate and management factors will complement our findings and elucidate whether their responses resemble or differ from those we describe here (Reed et al., 2006; Ficetola and Maiorano, 2016; Bruckerhoff et al., 2020; Glass et al., 2020). While we have focused here on local patterns of dickcissel population change, regional weather patterns also have important influences on migratory bird breeding population dynamics, and carry-over effects may also play a role. Thus, we encourage future studies of dickcissels and other migratory birds that track individuals through telemetry and other technologies throughout the annual cycle, as well as further inquiries into variation in the sex ratios of breeding dickcissels and their relationships to avian survival, productivity, and population dynamics. Finally, grassland conversion to agriculture remains a foremost threat to obligate grassland species, and protecting and managing grasslands is therefore an utmost conservation priority on dickcissels' and other migratory birds' breeding grounds as well as their migratory stopover and wintering areas.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

The animal study was reviewed and approved by the USGS Bird Banding Laboratory.

AUTHOR CONTRIBUTIONS

NA designed and supervised the project. DHK, NA, RHK, and AG collected field data. KMR and RHK organized the database with contributions from AG. KMR, SG, AS, and RHK analyzed data and produced tables and figures. NA and KMR wrote the manuscript with input from all other authors. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.536769/full#supplementary-material

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Warmer April Temperatures on Breeding Grounds Promote Earlier Nesting in a Long-Distance Migratory Bird, the Prothonotary Warbler

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Global climate change and warming are altering hemispheric and local weather patterns. Altered weather patterns have great potential to affect the phenology of life history events, such as the initiation of breeding in organisms that reproduce seasonally. Long-distance migratory birds may be particularly challenged by changes in local weather on breeding grounds because they arrive from distant locations and must commence breeding when conditions are appropriate. Here we explore the effects of local temperature on first egg dates and annual productivity in a long-distance Neotropical migratory songbird, the prothonotary warbler *Protonotaria citrea*. We present results from a 20-year (1994 to 2013) study documenting the detailed nesting activities of a color-marked population (average of 155 individual females each year) of warblers in southern Illinois, United States. The warblers typically arrive in April and start breeding in late April and May in our study system. We tested for an effect of local average April daily temperature and female age on first egg dates, total number of offspring produced per female, and the probability of fledging two broods. We found that warmer April temperatures promoted earlier first egg dates and higher average annual productivity in the warblers. On average, older females had earlier first egg dates than 1-year-old females, but both age groups responded similarly to local April temperatures. The reproductive gains associated with earlier first egg dates in warmer years stemmed from an increased probability of successfully fledging two broods, suggesting that earlier first egg dates do not currently create a mismatch with food (insect) resources. Earliest arrival dates of warblers to the region of our study system were not affected by local April temperatures, suggesting that females vary their first egg date based on conditions they experience/assess after their arrival. Whereas these birds currently adjust the timing of their breeding and actually produce more offspring in warmer years, continued global warming may eventually upset the current balance between arrival dates, food resources, and the commencement of nesting.

Keywords: first egg dates, global warming, local temperature effects, long-distance migratory bird, prothonotary warbler, *Protonotaria citrea*, reproductive output

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INTRODUCTION

Natural selection favors timing of reproduction that maximizes fitness. Favorable environmental conditions, availability of mates, and pulses in necessary food resources are some of the main factors shaping where and when to reproduce (Perrins, 1970; Bronson, 1985; Daan and Tinbergen, 1997; Verhulst and Nilsson, 2008). Animal migrations are behavioral and physiological wonders that have evolved to take advantage of geographically disparate resources that affect the timing and location of breeding events (Milner-Gulland et al., 2011; Winkler et al., 2014; Shaw, 2016). The breadth of taxa that migrate is expansive and includes insects, reptiles, fish, mammals and birds (Williams, 1957; MacKeown, 1984; Dingle, 1996; Holland et al., 2006; Newton, 2010; Southwood and Avens, 2010). Bird migrations cover thousands of kilometers, with many species moving between equatorial latitudes where they spend time on non-breeding grounds, and northern and southern temperate latitudes where they breed during hemispheric summers (Berthold, 2001; Newton, 2010). These temperate breeding seasons in migratory birds occur annually during pulses and peaks in food resources (often insects) that are enough to support both resident and migratory species as they attempt to reproduce (Alerstam, 1990; Greenberg and Marra, 2005; Thorup et al., 2017). The onset of long-distance migration to breeding grounds in passerines (i.e., songbirds) is controlled by endogenous circannual rhythms which are synchronized by changes in day length (i.e., photoperiod; Gwinner, 2003; Gwinner and Helm, 2003; Kumar et al., 2010). Once begun, it then takes days to weeks of flying and refueling (at stopover sites) for these migrating birds to reach their breeding grounds (Bowlin et al., 2005). Therefore, long-distance migrants are constrained in their ability to adjust their departure dates from non-breeding grounds based on what conditions are like on their breeding grounds (Both and Visser, 2001; Miller-Rushing et al., 2008; Fraser et al., 2013).

Global average temperatures are increasing, with significant rates of increase in the past half century (Hurrell and Trenberth, 2010; IPCC, 2013), and the potential for global climate change (warming) to disrupt or otherwise affect the timing of breeding in migratory birds is substantial (Dunn and Winkler, 2010; Visser et al., 2010; Cohen et al., 2018). Migratory birds are thought to be particularly vulnerable because they may not be able to adjust their breeding phenology as global temperatures increase (Strode, 2003; Mills, 2005; Miller-Rushing et al., 2008; Both et al., 2010). To the contrary, a growing body of research is finding that warming in temperate latitudes associated with global climate change is advancing the timing of clutch initiation in several species of migratory birds (e.g., Dunn and Winkler, 1999, 2010; Both et al., 2004; Mazerolle et al., 2011; Tomotani et al., 2018). Earlier nesting may be a byproduct of temperature-related advances in plant and insect phenologies experienced by birds upon arrival at breeding grounds (Townsend et al., 2013; Shave et al., 2019). However, earlier breeding can cause reductions in reproductive success if the timing of breeding creates a mismatch between seasonal pulses in critical resources (Both et al., 2010) (i.e., food) and peak demand for feeding young (Visser and Gienapp, 2019). For example, a long-term study of pied flycatcher *Ficedula hypoleuca* in the Netherlands found that the flycatchers started nesting earlier in response to global warming, but not enough to match earlier peaks in caterpillar abundance at some locations (Both and Visser, 2001). Flycatcher population declines in areas where the greatest mismatches occurred have been attributed to this dynamic (Both et al., 2006). Another study looking at arrival dates of 117 migratory bird species over five decades found that ecological mismatch was a general pattern among migratory birds breeding in northern Europe, possibly contributing to population declines (Saino et al., 2011). These mismatches can reduce individual fitness and population viability, and therefore drive evolution by favoring those individuals well-matched to peak resource availability (reviewed in Visser and Gienapp, 2019).

Resident (i.e., non-migratory) bird species are thought to be less susceptible to trophic mismatches than migratory species (Monkkönen et al., 1990; Both et al., 2010; Parejo, 2016). One reason is that the timing of nesting is plastic in some resident species, allowing individuals to adjust their breeding based on spring phenology (Charmantier et al., 2008). In addition, during the spring, non-migratory birds are already near where they are going to breed, making it easier for them to respond to warmer or colder springs (Pulido and Widmer, 2006; Knudsen et al., 2011). For example, in a population of year-round resident song sparrows *Melospiza melodia* in North America individuals initiated breeding earlier in warm springs, and produced more offspring as a result (Wilson and Arcese, 2003). In another example, a 47-year study of great tits *Parus major* breeding in nest-boxes in the United Kingdom found that mean first egg dates and caterpillar phenology both had advanced by about 14 days on the same study site (Charmantier et al., 2008). But not all resident bird species avoid mismatches. For example, a separate study of great tits over a 23-year period in the Netherlands found that the timing of reproduction had not advanced in step with warming temperatures and earlier peaks in availability of food for the young (Visser et al., 1998). In addition, one recent study of 21 British songbirds spanning 18 years found no evidence that the relationship between productivity and relative amount of mismatch varied with migratory distance status (Franks et al., 2018).

While resident species may by and large avoid mismatches, not all migratory birds suffer reduced fitness when breeding phenology is altered by warmer spring temperatures. In some instances, advanced breeding of migratory birds in warmer years resulted in increased reproductive output. For example, black-throated blue warblers *Setophaga caerulescens* in New Hampshire United States initiated breeding earlier in warmer springs, which increased the probability that individuals attempted a second brood and led to higher annual fecundity (Townsend et al., 2013). Similarly, in a study of reed warblers *Acrocephalus scirpaceus* in Poland, first egg dates were earlier in warmer springs, which increased the length of the breeding season and resulted in more opportunities to renest (Halupka et al., 2008). Both studies also noted that the abundance and diversity of insects available for consumption were not diminished or mismatched in warmer years. Therefore, mismatches may be less likely in environments and for species where food is relatively constant or abundant throughout the breeding season (Dunn et al., 2011). This highlights the importance of documenting how local weather (e.g., temperature) experienced on the breeding grounds by newly arriving migratory birds influences both the commencement of nesting (i.e., first egg dates) and reproductive output of individuals when looking for the presence of a mismatch.

Beyond the potential for there to be a trophic mismatch, migratory birds nesting earlier on temperate breeding grounds may experience local weather conditions (e.g., temperature and precipitation) that affect when and how successfully they reproduce (Dunn and Winkler, 2010). Unusual weather events, in general, tend to negatively impact breeding birds (Shipley et al., 2020). For example, some migratory species may start breeding earlier because of warm weather on breeding grounds, only to have subsequent colder and/or wetter weather cause adult mortality, or reduce reproductive success by decreasing incubation efficiency and nestling provisioning (Brown and Brown, 2000; Conway and Martin, 2000; Coe et al., 2015; Cox et al., 2019; Shipley et al., 2020). This is particularly true for aerial insectivores such as barn swallows *Hirundo rustica* and tree swallows *Tachycineta bicolor* where cold temperatures and precipitation can cause short-term food (insect) shortages linked to inadequate incubation and poor nestling growth (Coe et al., 2015; Cox et al., 2019), and for barn and cliff swallows *Petrochelidon pyrrhonota* where adults can starve when activity of flying insects is reduced by periods of cold and/or wet weather lasting four or more days (Brown and Brown, 2000). Breeding earlier at temperate latitudes, therefore, comes with some added weather-related risks.

Prothonotary warblers *Protonotaria citrea* are long-distance Neotropical migrants that breed seasonally at temperate latitudes in the eastern United States. The warblers are insectivorous but not highly specialized on one guild of insect (Petit et al., 1990a,b; Dodson et al., 2016; Petit, 2020), and they occur in bottomland and swamp forests where there is an abundant and diverse invertebrate biomass continuously emerging during the warbler's breeding season (Petit and Petit, 1996; Heinrich et al., 2013; Batzer et al., 2016; Dodson et al., 2016). Previous work on these warblers in our study system found no support for food to limit reproductive output, even when densities were manipulated to increase substantially (Hoover et al., 2020). One previous study of prothonotary warblers in the eastern part of their breeding range found changes in local spring temperatures not to have an effect on mean nest initiation dates, and for warmer spring temperatures to increase mean probability of attempting a second brood when older females were more abundant in the population being studied (Bulluck et al., 2013). Here we take a somewhat different approach by studying the effects of local spring temperatures on individual females' first egg dates, annual reproductive output, and the probability of fledging second broods. Given that the warblers breed in a food-rich habitat, it is possible that any local-temperature-driven annual adjustments in when nesting is first initiated would not necessarily have a negative effect on overall reproductive output.

Here, we investigate the effects of local temperature on first egg dates, annual productivity, and the probability of fledging two broods in prothonotary warblers using data collected during a 20-year period (1994-2013). Because local temperature trends are not always similar to global warming trends (Hansen et al., 2001), we compared our local April temperature data trend to the Annual Global Land Temperature Anomaly data trend (NOAA National Centers for Environmental information, Climate at a Glance: Global Time Series, published January 2020, retrieved on February 1, 2020 from https://www.ncdc.noaa.gov/cag/) for the period 1983 to 2019 to determine if local April temperatures reflected global temperature changes. The warblers arrive at our study system during April and commence nesting in late April and May (Hoover, 2001). Thus, we predicted that higher local average April daily temperatures (local April temperature hereafter) would result in earlier first egg dates in our study system. Based on prior observations (Hoover, 2001), we expected that, within a given year, older (>1 year old) females would have earlier first egg dates than the 1-year-old females that were breeding for the first time. To determine whether warmer spring temperatures were a cost or benefit to warbler productivity, we also tested for effects of local April temperature on the season-long reproductive output of the warblers and, related to that, the probability that females successfully fledged two broods. Finally, to determine if arrival dates of migrating warblers to the general area where our study took place were associated with local April temperatures, we compared earliest arrival dates (using eBird) to local April temperatures for the period 1999 to 2019.

MATERIALS AND METHODS

From 1994 to 2013, we studied the breeding ecology of individually marked prothonotary warblers on 14 discrete (i.e., separated from each other by >1 km) forested wetland study sites within a 192 km^2 portion of the Cache River watershed (centered at 37.294°N, 88.975°W) in southern Illinois, United States. The warblers migrate from non-breeding grounds in southern Central America and northern South America to breeding grounds in the eastern half of the United States from the Gulf of Mexico to the northern tier states and southern Ontario Canada (Petit, 2020). Prothonotary warblers are obligate secondary cavity nesters that breed over or near standing water in bottomland hardwood and swamp forests (Petit and Petit, 1996). They defend exclusive territories, are socially monogamous, readily accept nest boxes (Fleming and Petit, 1986), and adults exhibit high site fidelity between breeding seasons (Hoover, 2003a). Females build nests and incubate eggs, and both sexes provision nestlings and fledglings. During the breeding season, the warbler's diet is a diverse assemblage of insects including caterpillars (order Lepidoptera), flies and midges (order Diptera), spiders (class Arachnida), mayflies (order Ephemeroptera), and dragonflies (order Odonata) mostly gleaned from leaves, twigs, and branches (Petit et al., 1990a,b; Dodson et al., 2016; Petit, 2020). The warblers often attempt a second brood and on rare occasions fledge three broods in a single breeding season (Hoover, 2003a; Bulluck et al., 2013; Petit, 2020).

We monitored warblers that used artificial nest boxes placed on trees or metal conduit, located 50 to 100 m apart, within the 14 study sites (Hoover, 2003a). Prothonotary warblers used nest boxes almost exclusively (Hoover, 2003a; Hoover et al., 2020) and the nest boxes mimicked natural cavities in terms of nest predation and cowbird parasitism (Hoover, 2001). Nest boxes were monitored every 3–5 days from mid-April to early August each year. This frequency of nest monitoring allowed us to determine when egg laying and incubation commenced, clutch size, and hatching success. Nests were typically visited two to three days prior to fledging and warbler nestlings were banded with a uniquely numbered aluminum leg band (U. S. Geological Survey). The number of warbler fledglings assigned to each nesting attempt was the number of nestlings present at that pre-fledging visit so long as the nest was intact and the adult warblers were seen with, or behaved as though they had, recently fledged warblers in their territory the very next visit post-fledging (Hoover, 2003b, 2006). Warbler nests are often parasitized by brown-headed cowbirds *Molothrus ater* (Hoover, 2003b; Hoover and Reetz, 2006), and we noted the number of cowbird eggs, nestlings and fledglings associated with each nesting attempt.

We were unable to document arrival dates of individual warblers to our study system. Nearly all females in a given year were not observed until they were building a nest in a given nest box. We captured all adult birds that used nest boxes and banded each with a unique combination of a single numbered aluminum leg band and multiple colored plastic leg bands. We captured and/or re-sighted (for those already banded) birds to identify the individual male and female associated with each nesting attempt each year. We captured females while they were incubating by placing our hand over the opening of an active nest box, trapping the female inside. Females exited the nest box into a clear plastic bag placed over the opening and were removed from the bag immediately for processing. We captured males by placing a male decoy warbler paired with a playback of a warbler song in front of a mist-net within each male's territory. Upon capture of adults, we measured body mass (g), wing chord length (mm), and tarsus length (mm) of each individual. For individuals captured for the first time, we used these measurements along with plumage characteristics to determine their age [second-year (SY; i.e., 1 year old and entering their first breeding season) vs. after-second-year (ASY; i.e., ≥2 years old) (see Kowalski, 1986; Pyle et al., 1987). We also knew the age of warblers we had banded as nestlings that returned in subsequent years to breed in our study system. For nearly every individual female breeding on our study sites in a given year we were able to document her first egg date, age, total number of offspring produced, and whether or not she fledged two broods.

Temperature Data

Our focus for comparison with average first egg dates and reproductive output of prothonotary warblers was the local temperature during the month of April when warblers arrive at our study system. Local temperature data for 1994 to 2013 were obtained using archived weather data from a nearby weather station (∼ 30 km south of study system; https://www.wunderground.com/history/monthly/us/ky/west-paducah/KPAH/date). We used the mean value of average daily temperature (°C) measurements from the entire month of April each year as our metric of local temperature because the warblers initiate nesting in late April and May. To simply determine that our local April temperatures trended similarly to global temperatures we considered a longer run of years (1983 to 2019), and used the above source for the local temperatures and Annual Global Land Temperature Anomaly data from the National Oceanic and Atmospheric Administration (NOAA National Centers for Environmental information, Climate at a Glance: Global Time Series, published January 2020, retrieved on February 1, 2020 from https://www.ncdc.noaa.gov/cag/). These global data are the departure of annual global land temperature (for a given year) from the average of 1901–2000 values (values are °C; positive and negative values represent warming and cooling, respectively).

First Arrival Data

To determine if there was a relationship between local April temperatures and earliest arrival dates of migrating warblers to southern Illinois during 1999 to 2019, we used data from eBird (https://ebird.org/map). We selected the months of March-April for each year and noted the earliest reported sighting(s) along the Gulf Coast (from Houston, Texas to Tallahassee, Florida) and in the southern Illinois region (just north of the Ohio River) where our study took place. These arrival dates are those of male prothonotary warblers, which often arrive earlier than females or are more likely to be observed because they are more conspicuous than females (Hoover, 2001; Petit, 2020). We lack detailed arrival dates for females breeding on our study sites, thus we used this approach with eBird data to determine whether local earliest arrival dates and local temperatures were correlated, whether local earliest arrival dates and those for along the Gulf Coast of the United States were correlated, and whether first eggs dates were correlated with local first arrival dates.

Statistical Analysis

We used SAS 9.4 software (SAS Institute, 2013) to construct and fit all models. Prior to fitting all models, we examined the residuals of response variables to check for normality. Values reported in the results section are means ± SE unless otherwise indicated. We report the type-III fixed effects test statistics and p-values and set $\alpha = 0.05$. We first used simple linear regression (i.e., the 'genmod' procedure) analyses to determine if any trends (i.e., increasing, decreasing, or no trend) existed between our local April temperatures or Annual Global Land Temperature Anomaly values and year (1983 to 2019).

We next used a general linear mixed model (i.e., the 'mixed' procedure) to examine the influence of local April temperatures on warbler first egg dates. Fixed effects included local April temperature and female age (category: 1-year-old versus older). Random effects included Female ID as a random intercept with year as the random slope, and study site as a separate random intercept. Female age was included as a fixed effect because after-second-year (older) females tend to arrive and begin nesting earlier than second-year (1-year-old) females (Hoover, 2001; Petit, 2020). Warblers are relatively long-lived (i.e., up to 13 years, unpublished data) and exhibit high site fidelity between years (Hoover, 2003a) thus we expected numerous data points for each individual across years. Because we studied females across 14 distinct study sites within our study area, we included study site as a random effect to account for variation among study sites.

We used a generalized linear mixed model (i.e., the 'glimmix' procedure) with a negative binomial distribution and log-link function and a Laplace approximation to determine whether local spring temperatures influenced the number of warbler fledglings produced per female per year (annual productivity hereafter). Fixed effects included local average April temperature and female age. Random effects included a random intercept of female ID with year as a random slope, and a random intercept of study site with the categorical term tree/poles as a repeated effect. The tree/pole variable described whether most boxes within a given study site in a given year were installed on trees or metal conduit. Throughout the course of this study we used metal conduit to reduce nest predation for various unrelated experiments and thus wanted to control for this effect in our modeling of annual productivity. We incorporated the additional tree/pole categorical variable as a repeated measure on study site as most study sites had both categories represented at some point throughout the study. We also know that cowbirds reduce warbler productivity in very predictable ways (Hoover, 2003b), thus prior to constructing our model we used a regression analysis to determine if the average number of cowbird nestlings per female warbler per year was affected by local April temperatures. The average number of cowbird nestlings per female warbler per year was not affected by local April temperatures ($F_{1,19} = 0.24$, $P = 0.63$, $r^2 = 0.01$) so we did not consider brood parasitism by cowbirds further in this study.

Previous research in our study system demonstrated that females that nest earlier are more likely to attempt second broods (Hoover et al., 2020). Thus, local warmer April temperatures could also increase the probability of females successfully fledging two broods and explain any increases in productivity we observed. To test this prediction, we used a generalized linear mixed model (i.e., the 'glimmix' procedure) with a binomial distribution and logit-link function using a Laplace approximation, the fledging of two broods (no, yes) as the response variable, and female age and local April temperatures as fixed effects. Random effects again included a random intercept of female ID with year as a random slope, and a random intercept of study site with the categorical term tree/poles as a repeated effect.

In all mixed models where we used random effects with a repeated measure or random slope design, we tested three separate variance-covariance structures to see which structure best fit the data. For this, we compared variance components (i.e., default in SAS), unstructured, and compound symmetry structures and then compared the AICc values to find the best variance-covariance structure given the data. In all cases, the default variance components structure provided the lowest AICc value and thus the best fit. In all models where we compared the variance-covariance structures, the outcomes for our variables of interest were qualitatively the same. Lastly, we used simple linear regression analyses to determine if the earliest warbler spring arrival in southern Illinois (based on eBird.org) was influenced by local April temperature or earliest arrival dates of warblers to the Gulf Coast states; and whether first egg dates were associated with earliest arrival dates to southern Illinois.

RESULTS

During the period 1994 to 2013 we obtained 3,136 first egg dates, annual productivity values, and double-brooding statuses, from 2,017 individual female prothonotary warblers nesting in our study system. Individual female warblers were sampled in anywhere from 1 to 6 different years during the study. Annual values for local average April daily temperature, mean first egg dates, and mean annual productivity are provided in **Table 1**.

During the period 1983 to 2019, both the local April temperature ($F_{1,35} = 17.2$, $P < 0.001$, $r^2 = 0.33$) and the Annual Global Land Temperature Anomaly ($F_{1,35} = 156.8$, $P < 0.001$, $r^2 = 0.82$) increased significantly with year (**Figure 1**). This shows that our local temperature pattern was similar to temperature trends at a global scale during the same time period.

The range of values for first egg dates across all individual females was ordinal dates 107 (17 April) to 157 (6 June). Both average April daily temperature and female age had significant effects on first egg dates of prothonotary warblers. First egg dates became earlier as local April temperatures increased ($F_{1,3045} = 100.8$, $P < 0.001$) and were earlier for older females (i.e., $>$1-year-old) compared to 1-year-olds ($F_{1,3125} = 153.7$, $P < 0.001$) (**Figure 2**). First egg dates for older females, on average, were approximately 4 days earlier than young females in a given year. Across the spectrum of local April temperatures occurring during our study, mean first egg dates varied by approximately 9 days, from older females in years with warmest April temperatures to young females in years that were coldest (**Figure 2**).

Across all individual females in our study, the range for annual productivity was 0 to 14 warbler fledglings produced. Annual productivity of female warblers was affected significantly by average April daily temperature, female age, and when sites had boxes on metal conduit. The number of warbler fledglings produced increased as local April temperatures increased ($F_{1,1097} = 22.8$, $P < 0.001$) and was greater for older females (i.e., $>$1-year old) compared to 1-year-olds ($F_{1,1097} = 19.9$, $P < 0.001$) (**Figure 3**). For young and older females alike, reproductive output increased by approximately 0.7 fledglings across the range of April temperatures experienced, with older females producing on average 0.5 more fledglings per year compared to young females (**Figure 3**). As we expected, females nesting on sites where most nest boxes were installed on metal conduit produced 0.63 ± 0.23 (SE) more warbler fledglings in a given year on average compared to those nesting where most nest boxes were on trees ($Z = 2.8$, $P = 0.003$). In addition, females were more likely to produce two broods in warmer years ($F_{1,3133} = 11.0$, $P < 0.001$) (**Figure 4**). On average, older females were nearly twice as likely as younger females to produce two broods ($F_{1,3133} = 25.9$, $P < 0.001$).

Earliest male arrival dates to southern Illinois based on eBird data during the period 1999 to 2019 were not related to local April daily temperatures ($F_{1,19} = 0.4$, $P = 0.51$, $r^2 = 0.02$) (**Figure 5**).

TABLE 1 | Summary data for prothonotary warblers nesting in the Cache River watershed in southern Illinois, United States during 1994–2013. Ordinal date 121 = 1 May.

Year	Females (n)	Average April daily temperature (°C)	Ordinal date of first egg ($\bar{X}$ ± 1SE)	Fledglings produced per female ($\bar{X}$ ± 1SE)
1994	48	16.1	124.5 ± 0.86	3.90 ± 0.42
1995	79	15.6	127.4 ± 0.74	2.92 ± 0.26
1996	98	12.2	131.1 ± 0.59	1.83 ± 0.25
1997	121	11.1	132.5 ± 0.48	2.21 ± 0.23
1998	157	13.3	127.1 ± 0.37	1.63 ± 0.19
1999	111	15.6	126.0 ± 0.46	3.16 ± 0.28
2000	88	13.3	127.6 ± 0.55	3.03 ± 0.29
2001	66	17.2	121.3 ± 0.68	2.95 ± 0.29
2002	36	15.6	128.2 ± 1.45	4.83 ± 0.42
2003	81	15.6	125.9 ± 0.78	4.90 ± 0.37
2004	170	14.4	125.0 ± 0.52	4.08 ± 0.23
2005	227	14.4	128.2 ± 1.45	3.24 ± 0.16
2006	300	17.2	124.8 ± 0.48	3.86 ± 0.16
2007	247	13.3	131.0 ± 0.42	3.54 ± 0.17
2008	165	13.3	134.1 ± 0.71	3.74 ± 0.16
2009	276	15.0	126.0 ± 0.40	3.40 ± 0.15
2010	228	16.7	127.0 ± 0.40	3.50 ± 0.16
2011	188	16.7	138.8 ± 0.53	4.36 ± 0.18
2012	240	16.1	129.0 ± 0.60	2.58 ± 0.14
2013	219	13.3	128.8 ± 0.65	3.10 ± 0.18

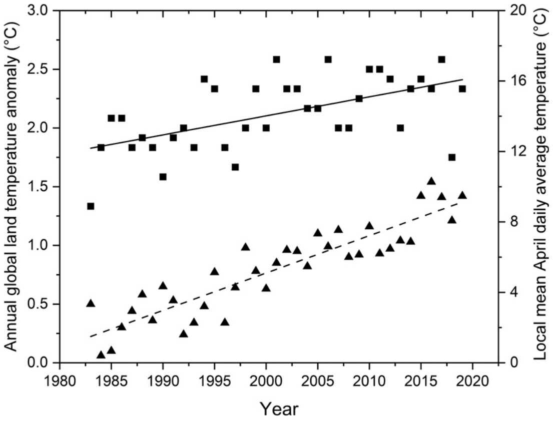

FIGURE 1 | Local April temperatures for southern Illinois, United States (squares and solid line) and Annual Global Land Temperature Anomaly values (triangles and dashed line) significantly increased during 1983 to 2019. Shown are the data points for each year and best fit lines for the regressions of the local and global parameters on year.

Arrival dates for warblers in southern Illinois tended to be earlier when arrivals to the Gulf Coast states were later ($F_{1,19} = 3.6$, $P = 0.07$, $r^2 = 0.16$). During the period 1999 to 2013, first egg dates were not related to earliest local arrival dates ($F_{1,13} = 0.08$, $P = 0.79$, $r^2 = 0.01$).

DISCUSSION

We found that similar to global warming trends, local April temperatures in southern Illinois are also increasing over time.

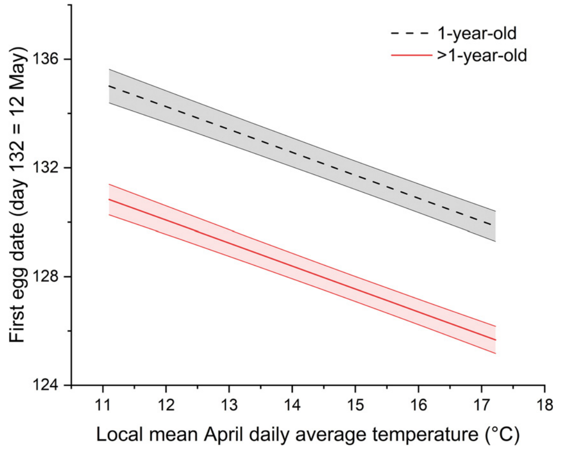

FIGURE 2 | First egg dates of prothonotary warblers are earlier when local April temperatures are warmer and for older females in the Cache River watershed, IL, United States during 1994 to 2013. Shown are model output best fit lines including random effects held at their mean values. Shaded regions around best fit lines are ± 1 SE.

Prothonotary warblers in our study system began nesting earlier and produced more offspring in years when local April temperatures were higher. As expected, older females started earlier and produced more offspring than first time breeders likely because of the earlier arrival dates of non-yearlings. The result of higher annual productivity in warmer years when nesting begins earlier suggests that the local warming trend has not yet created a mismatch between the timing of nesting and availability of food resources. We also found that local April temperatures did not influence earliest warbler arrival dates

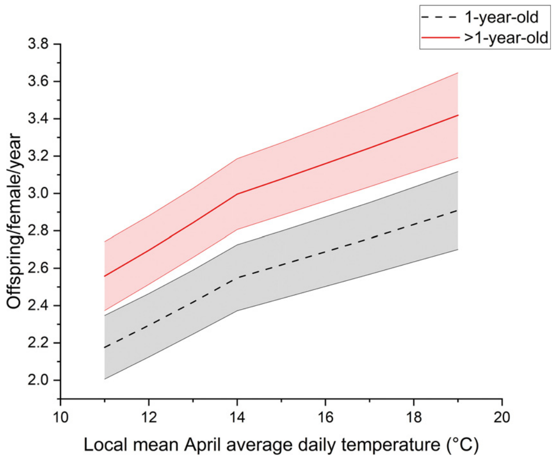

FIGURE 3 | Fledglings produced per female prothonotary warbler per year increased with local April temperatures and female age in the Cache River watershed, IL, United Sttaes during 1994 to 2013. Shown are model output best fit lines including random effects held at their mean values. Shaded regions around best fit lines are ± 1 SE.

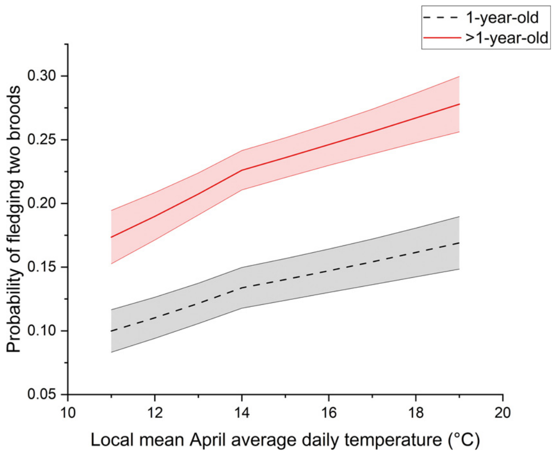

FIGURE 4 | The probability of producing two broods increased with local April temperatures and female age in the Cache River watershed, IL, United States during 1994 to 2013. Shown are model output best fit lines including random effects held at their mean values. Shaded regions around best fit lines are ± 1 SE.

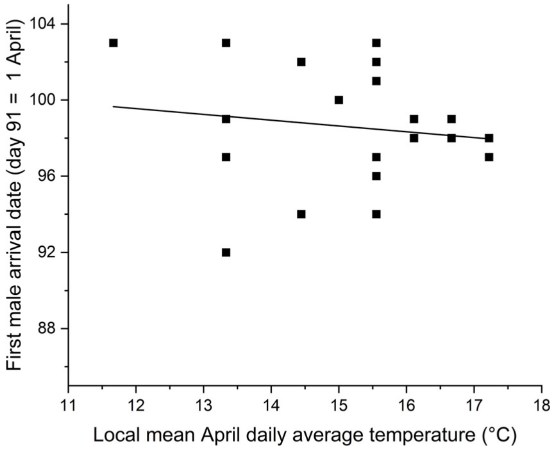

FIGURE 5 | Earliest male prothonotary warbler arrival dates to southern Illinois, United States were not affected by local April temperatures during 1999 to 2019. Shown are the data points for each year and the best fit line for the regression of arrival dates on local April temperatures.

in southern Illinois. Taken together, these results show that prothonotary warblers are flexible in their timing of breeding and that current warming trends may prove beneficial to our local population at least in the short term.

Warblers with earlier first egg dates had higher annual productivity in our study even under scenarios where predators were not excluded. The likely reason for this is that earlier breeding associated with warmer temperatures resulted in an increased probability of fledging two broods within a given breeding season. An increase in attempting second broods previously had been documented in our study system (Hoover et al., 2020), as well as in a study of prothonotary warblers in Virginia, United States (Bulluck et al., 2013). Similar patterns of increased double brooding, or increased chances of successfully producing a replacement brood, as a byproduct of nesting earlier in warmer years has also been found in other species (Halupka et al., 2008; Monroe et al., 2008; Verhulst and Nilsson, 2008; Townsend et al., 2013). A study of 20 bird species in Denmark found warmer temperatures to lengthen the breeding season for those species capable of producing multiple broods (Møller et al., 2010), and increase the probability of individuals to attempt second broods. Other examples include research on black-throated blue warblers in New Hampshire, United States (Townsend et al., 2013) and reed warblers in Poland (Halupka et al., 2008), where individuals breeding earlier in warmer years had higher annual fecundity because they were more likely to attempt multiple broods (both studies) or multiple re-nests (reed warblers), and both studies noted that double-brooding and re-nesting were supported by ample and diverse insects (i.e., food) being available. To produce more offspring requires abundant food resources throughout the breeding season, and abundant insects are a hallmark of the bottomland and swamp forests where the prothonotary warblers nest (Petit and Petit, 1996; Heinrich et al., 2013; Batzer et al., 2016; Dodson et al., 2016). Food resources (insects) in the forested wetlands and swamps where the warblers prefer to nest can even be supplemented by the terrestrial habitats found in bottomland forest ecosystems (Nakano and Murakami, 2001; Baxter et al., 2005). Differences in warbler clutch sizes likely contributed little to the trend in annual productivity we report here because the vast majority of warbler first clutches contain five warbler eggs in any given year (Hoover, 2001, 2003b; Hoover et al., 2020). In terms of age effects, even though the young female warblers on average started later and produced fewer total fledglings than the older females, the general effects of local April temperatures on first egg dates and annual productivity in young females were similar to the older females (**Figures 2–4**).

Advanced first egg dates of migratory birds in warmer years may be a byproduct of earlier arrival dates. However, global warming has no effect on photoperiod and should have little effect on when migratory birds using these cues depart for their breeding grounds. Indeed, the ability of long-distance migrant bird species to adjust first egg dates (i.e., breeding phenology) in response to environmental factors is thought to be constrained by limitations associated with the timing of migration (Strode, 2003; Miller-Rushing et al., 2008, Both et al., 2010). Yet, several studies have documented earlier arrival of migratory birds to breeding grounds in years when temperatures on breeding grounds were warmer, or even when temperatures on non-breeding grounds were warmer prior to spring migration (Cotton, 2003; Usui et al., 2017). In a meta-analysis covering 73 published studies and 413 species, Usui et al. (2017) found a robust pattern where earlier arrivals in warmer years were not dependent on whether temperatures represented changes at breeding, passage or non-breeding sites, or whether arrival was to the breeding or passage grounds. In another meta-analysis of arrival dates of 20 migratory bird species breeding in Oxfordshire, United Kingdom, Cotton (2003) found that arrival dates became earlier with increases in a continental-scale temperature measurement taken from their non-breeding grounds (winter sub-Saharan African temperature anomaly), suggesting that some migratory birds may begin their migrations earlier when it is warmer on the non-breeding grounds. Counter to these patterns of earlier arrival in warmer years, arrival dates of several species of long-distance migratory wood warblers to breeding grounds in Illinois (100-year period) and Minnesota (40-year period) United States were not correlated with local spring temperatures (Strode, 2003). Earliest arrival dates of prothonotary warblers to southern Illinois, as determined using eBird data, varied among years but showed no relation to local April temperatures. Differences in arrival dates may explain, however, why older females in our study system had earlier first egg dates on average. Female warblers are relatively cryptic (no singing and not boldly colored) during the breeding season (Petit, 2020). While we do not have good data on specific arrival dates of individuals across years in our study system, we have noticed that the vast majority of the earliest females we happen to observe in the spring prior to the commencement of nesting are banded individuals captured in a previous year (Hoover, 2001), which places them in the older age category.

While the aim of our investigation here was to document whether or not local spring temperatures affected first egg dates and season-long reproductive output in prothonotary warblers, how and why the warblers nest earlier and produce more offspring in warmer years remains to be determined. Even if arrival dates were constrained by departure dates from wintering areas, there could still be flexibility in when breeding begins after arriving on breeding grounds. It is possible that arrival dates are similar across years but latency to laying first eggs is shortened in years when local temperatures are warmer and lengthened when cooler (Both and Visser, 2001; Visser et al., 2004). Arrival dates for individual females are a critical missing piece. To adequately document age-related patterns in arrival dates and whether arrival dates contribute to explaining earlier first egg dates when temperatures are warmer, we need to collect additional detailed information on arrival dates and settlement patterns of individual females in our study system in years with warmer and colder springs. These data for individual females, particularly those that breed across several years in our study system, would allow us to better understand whether evolutionary changes versus changes due to phenotypic plasticity (i.e., individual flexibility) are influencing the pattern between first egg dates and local April temperatures we observed (Charmantier et al., 2008; reviewed in Charmantier and Gienapp, 2014). If individuals are flexible in when they lay their first egg relative to local temperatures, then population mean first egg dates may trend earlier as temperatures trend warmer over several years, but still vary considerably between consecutive years that are warmer and colder (Charmantier et al., 2008). Our results suggest that individual females in our study population are flexible in their ability to adjust first eggs dates from year to year, depending on the local temperature, but specific data to verify this are still needed.

In a number of songbird species, breeding earlier in the season can have numerous benefits including producing offspring that are larger at fledging, and are more likely to be recruited into the breeding population (Wheelwright et al., 2003; Müller et al., 2005, Tarof et al., 2011). In our study system, warbler nestlings fledging earlier in the season have a higher first-year survival rate and likelihood of local recruitment than those produced later (McKim-Louder et al., 2013). Tomotani et al. (2018) found a similar pattern in a population of European pied flycatchers and attributed the higher recruitment of fledglings from earlier nesting attempts to fledglings having more time to develop prior to migrating to non-breeding grounds. The warbler young produced in our system return locally to breed (McKim-Louder et al., 2013) and may therefore be fairly well-adapted to local conditions. It remains to be seen if continued warming and even earlier fledging translates into similar or even higher recruitment rates, or possibly alters natal dispersal patterns that could contribute to expected shifts in species' breeding ranges (Parmesan and Yohe, 2003; Visser et al., 2009; Langham et al., 2015; Stephens et al., 2016).

Along with earlier nesting, higher local temperatures can alter plant phenology (i.e., earlier bud break and leaf out) (Schwartz et al., 2006; Richardson et al., 2013) and cause earlier insect emergence (Roy and Sparks, 2000; Both et al., 2006; Charmantier et al., 2008; Hodgson et al., 2011; Jamieson et al., 2012; but see Primack et al., 2009). The greatest demand for resources occurs when birds are feeding nestlings/fledglings (Nilsson, 1994; van Noordwijk et al., 1995; Both et al., 2009) and it is therefore advantageous for birds to initiate nesting so that peaks in insect availability match the demands of provisioning a brood or broods. Mismatches occur when environmental factors such as warming temperatures cause a misalignment of peak food demand and peak food availability (Thomas et al., 2001; Visser and Both, 2005; reviewed in Both, 2010; Dunn and Winkler, 2010). Had earlier breeding by the warblers in warmer years resulted in a mismatch with food resources, we would have expected to see a decrease in season-long reproductive output, rather than our observed increase. While we did not measure insect abundance, or how it varies seasonally and in relation to temperature, recent work in our system (Hoover et al., 2020), where densities of breeding warblers were manipulated higher, found no evidence for reproductive output to be food limited. In that study we found no significant effects of density or a density by date interaction on measures of reproductive output within a breeding season even with nearest-neighbor densities (i.e., pairs within 200 m of focal pair) exceeding 20 pairs. We suspect that abundant food (insect) resources known to occur in bottomland forest ecosystems (Baxter et al., 2005; Batzer et al., 2016), in conjunction with the diverse diet of the warblers (Petit, 2020), reduces the risk that temperature-related shifts in their first egg dates might result in a mis-match. It is also possible that the emergence and abundance of relevant insects is shifted earlier in warmer years, similar to warbler first egg dates and what has been found in black-throated blue warblers in New Hampshire, United States (Townsend et al., 2013), as well as in great tits in the United Kingdom (Charmantier et al., 2008). Regardless, there are much more data needed from our study system to fully understand the dynamics between spring temperatures, arrival dates of individual females, and plant, insect and breeding phenologies.

Species or individuals not able to adjust the timing of their own breeding to match changes in resource peaks, or that tend to specialize on few types of food resources may be especially vulnerable to resource mismatches associated with global warming (Both et al., 2006; Møller et al., 2008; Both, 2010; Charmantier and Gienapp, 2014). Prothonotary warblers do not belong to either of these categories of vulnerable species. Similarly, breeding earlier in warmer years with no apparent cost to reproduction has been documented in many other migratory bird species including reed warblers (Halupka et al., 2008), tree swallows (Dunn et al., 2011), purple martins *Progne subis* (Shave et al., 2019), and black-throated blue warblers (Townsend et al., 2013). In each of these study systems, authors suggested that earlier breeding was not costly, in part, because food resources (i.e., insects) were available enough to accommodate it.

Apart from food availability, it is possible that continued global warming could hasten late-season dewatering of forested wetlands and swamps that are home to prothonotary warblers, thereby reducing the suitability of the habitat or exposing later season nests to increased nest predation (Hoover, 2006). Global warming could also exacerbate the threats prothonotary warblers already face from the loss, fragmentation, and hydrologic degradation of bottomland forest habitats (Hoover, 2009; Robinson and Hoover, 2011). In addition, while breeding was the focus of our study and is essential to species persistence, it is only one stage in the complicated life cycles of migratory birds.

The overall effects of global warming remain particularly difficult to predict for migratory species because they have complex habitat needs throughout their life cycles and complex physiological adaptations that coincide with timing of migrations (Winkler et al., 2014). For example, the effects of global climate change on the quality and distribution of suitable habitats may be very different for migratory pathways, stopover locations and non-breeding grounds used by migrants, potentially undermining the timing of events that have evolved to get migrants to their destination when resources are adequate to meet needs. Thus, much more information is needed, particularly for migratory species, on how global warming affects other annual cycle stages beyond reproduction (Hostetler et al., 2015; Culp et al., 2017; Tomotani et al., 2018). The prothonotary warbler is one example where warming temperatures currently are providing fitness benefits on local breeding grounds. The mobility of migratory species in general may make them more capable of adapting to a changing environment provided that any changes in the phenology of their life stages match any changes in the phenology of critical resources. With substantial warming in the Northern Hemisphere during the warbler's breeding season projected to continue in the coming decades (Vogel et al., 2019), it remains to be seen if and when a tipping point may be reached whereby earlier nesting no longer conveys a reproduction advantage.

DATA AVAILABILITY STATEMENT

The datasets generated and analyzed for this study can be found in the Illinois Data Bank https://doi.org/10.13012/B2IDB-6482573_V1.

ETHICS STATEMENT

The studies involving prothonotary warblers were conducted in compliance with Animal Research Protocols N6C107/7093, N8C046, 07040, 07224, 10011, 10013, and 10173 (each approved by the Institutional Animal Care and Use Committee of the University of Illinois at Urbana-Champaign, United States), Illinois State Lands and Nature Preserves Permits, United States Fish and Wildlife Service Permit number MB815400-1, and United States Geological Survey Banding Permit number 06507.

AUTHOR CONTRIBUTIONS

JH and WS formulated the questions, collected the data, supervised research and analyzed the data. Both authors contributed to the article and approved the submitted version.

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REVIEW
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Climate as an Evolutionary Driver of Nest Morphology in Birds: A Review

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Avian nests are critical for successful reproduction in birds. Nest microclimate can affect egg development, chick growth and fledgling success, suggesting that nest building behavior should be under strong selective pressure to nesting conditions. Given that the internal microclimate of the nest is critical for avian fitness, it is expected that nest morphology is shaped by the local environment. Here we review the relationship between nest morphology and climate across species' distributions. We collate growing evidence that supports a link between environmental conditions and particular nest traits, within species and across species. We discuss the degree to which phenotypic plasticity in nesting behavior can contribute to observed variation in nest traits, the role of phylogenetic history in determining nest morphology, and which nest traits are likely to be influenced by climatic conditions. Finally, we identify gaps in our understanding of the evolution of nest morphology and suggest topics for future research. Overall, we argue that nests are part of the extended phenotype of a bird, they play a crucial role in their reproductive success, and may be an important factor in determining which species will be able to persist in the face of ongoing climate change.

Keywords: nest microclimate, environmental condition, phenotipic plasticity, extended phenotype, evolution

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IN A NUTSHELL

- Birds build nests that are suitable for maintaining the ideal microclimate conditions for egg and chick development.
- We discuss the diversity of nest morphologies found among species and individuals.
- We show considerable evidence of building adaptations in nest size, lining and composition to local climate conditions.
- We suggest future research ideas to improve our understanding of how bird nest building behavior evolved.

INTRODUCTION

The role of environmental variation in the evolution of animal traits has been the subject of extensive study. There are hundreds of examples of selection on traits to various environmental conditions (Guidi et al., 2016; Meachen et al., 2016; Alhajeri and Steppan, 2018), such as beaks in Darwin's finches and malagasy vangas that have diversified in different environments (Reddy et al., 2012; Lamichhaney et al., 2015). In the same way that selection acts on phenotypes generating adaptations, selection should exert pressure and influence the evolution of traits that arise from behaviors and are extrinsic to species' phenotypes (extended phenotypes), such as birds' nests (Mainwaring, 2015).

Nests are ephemeral structures but they are fundamental for species' persistence (Hansell, 2000). They are built by parents to provide an optimal environment for their progeny, and several studies have shown that the conditions inside nests can dramatically affect offspring survival (Heenan, 2013; Mainwaring et al., 2014; DuRant et al., 2019). Therefore, nest morphology can be considered a phenotypic trait that should be subject to variation and driven by selection on nest building behavior of parents, like other traits that affect fitness.

There is a tight association between avian reproductive success and the climatic conditions inside the nest (microclimate) (Collias and Collias, 1984). An optimal nest microclimate influences the length of the incubation and nestling periods, which in turn affects parental condition and investment, hatching synchrony and brood size (Lombardo et al., 1995; Ardia et al., 2010; Griffith et al., 2016; Mueller et al., 2019). Nest microclimate can promote optimal embryonic development at the egg stage which enhances brood performance and chick survival (Durant et al., 2013a; Ospina et al., 2018). This is because temperature and humidity that are outside the species' tolerance range can compromise chick growth (body mass and structural size), influence microbial activity and water loss from eggs, as well as affect innate immunity, thermoregulatory and motor performance, and even sex ratios (Lombardo et al., 1995; Ardia et al., 2010; Deeming, 2016; Rodríguez and Barba, 2016; Larson et al., 2018; Wada et al., 2018; Belnap et al., 2019; Merrill et al., 2019). When incubation and brooding conditions have such fitness consequences, selective pressures that guarantee a suitable nest microclimate are expected to be high (Hansell, 2000; Greno et al., 2008; Hepp and Kennamer, 2012).

Indeed, parents also alter incubation behavior in relation to time of day, time in the season, embryo age, ambient temperature and precipitation (Feldheim, 1997; Álvarez and Barba, 2014; McClintock et al., 2014; Walters et al., 2016; Carroll et al., 2018). Parental behavior is integral to mitigating the effects of weather at the nest, especially extreme weather events, such as heavy rain, flooding or abnormal temperatures (Burger, 1978; Clauser and McRae, 2017). In hot, arid environments, for instance, clutch overheating poses great threats to egg survival and parents modify the duration and frequency of incubation bouts to minimize absences at the nest (Mougeot et al., 2014) and shade eggs to prevent eggs from overheating (Clauser and McRae, 2017). Egg arrangement in the nest and the frequency of egg-turning can also alter cooling/warming rates (Šálek and Zárybnická, 2015). It has been shown that egg turning can be more frequent in unshaded nests and eggs on the edges that are more prone to temperature variation are moved more often (Šálek and Zárybnická, 2015; Kelsey et al., 2016). However, any form of nest structure *per se* (e.g. cup nest or mat of vegetation versus scrapes on the ground) has important influence on clutch microclimate. Deeming (2011) has shown that humidity within cup nests is more stable across species' latitudes with distinct levels of humidity than in scrapes. Eggs on scrapes are particularly exposed to the environment, and parents must compensate for weather adversities (Collias and Collias, 1984). In fact, it has been suggested that it is less energetically costly for parents to invest in building a thermally suitable nest to promote optimal development, than to invest in behavioral compensation during incubation (Mainwaring and Hartley, 2013); a suitable nest with stable microclimate optimizes heat exchange in incubating parent/s and reduces heat loss or gain in eggs during parental absence, thereby reducing parental investment (Smith et al., 1974; Collias and Collias, 1984; Reid et al., 2000).

In this review, we aim to highlight the potential role of climate in the evolution of nest building behavior and consequently, nest morphology. We introduce the topic by briefly examining the traits that we use to define nest morphology and discuss to what degree the phylogenetic history of these traits determines their potential to respond to climatic pressures. From there we move on to a discussion of the mechanisms that drive variation in nest construction with special focus on local climate and we suggest topics for future research on the evolution of nest morphology.

To gain insights into how ubiquitous the association between nest morphology and the local climate is, we used the Web of Science (1945–2020) database to search for papers in English on bird nest microclimate and structure, that contained the words: bird and nest temperature or nest structure. Of 1,290 records rendered by this search, 52 papers investigated explicitly the relationship between the climate and nest building adaptations. From these, 88% report significant associations (19.7% of those with humidity and temperature, 13% with humidity only and 56% with temperature only, the remaining showed nest morphology variation across seasons and distributions but did not infer the role of climate). Of the total, 65.4% of studies were of a single species, 34.6% included more than one species, and only 22.2% of those used phylogenetic comparative methods to address broad evolutionary questions on nest building behavior (**Supplementary Table 1**). As we examine the associations between nests and environment, we explore the extent to which nest building behavior responds to selective pressures and propose new research questions to gain further insights into the relationship between nest and environment. Moreover, although this review focuses on compiling evidence for the role of climate in nest morphology, we also discuss other selective forces that, in conjunction with climate, have the potential to shape nest morphology evolution.

DEFINING THE MORPHOLOGY OF A NEST

Before we consider the role of climate in shaping nest morphology, it is important to clarify how we define nest morphology and the phylogenetic history of the traits involved. We use "nest morphology" to refer to the general nest structure, which is comprised of shape, size, lining, and composition. Like many other structures, it is hard to accurately describe a nest in a single dimension, given the diversity of nest morphologies and their component materials. This complexity reflects the general consensus that all aspects of nest morphology should be taken

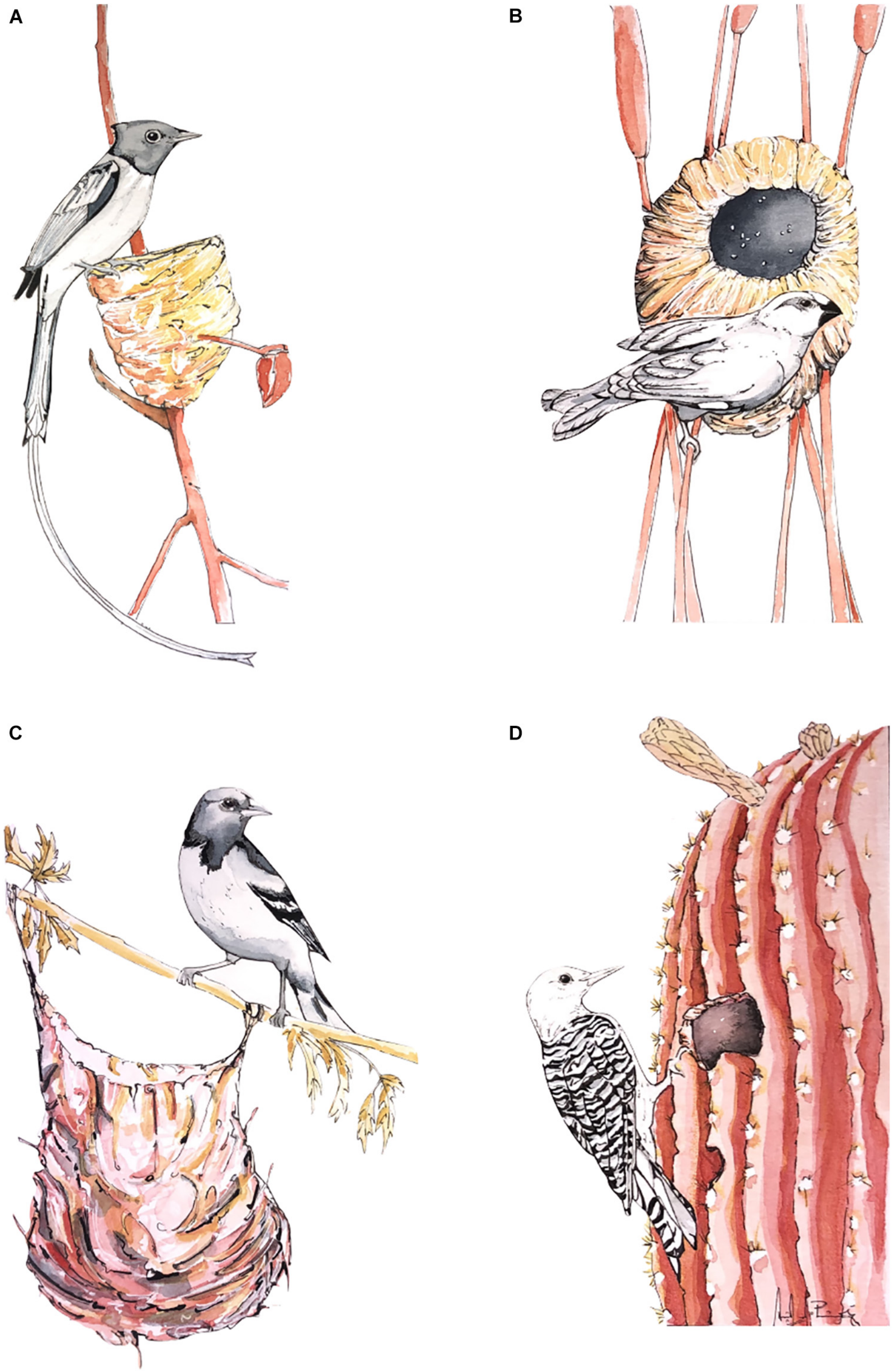

FIGURE 1 | Bird nest shape classification **(A)** supported cup from *Terpsiphone mutata*; **(B)** dome from *Amblyospiza albifrons*; **(C)** suspended cup (pouch) from *Icterus galbula*; **(D)** cavity from *Melanerpes uropygialis*. Colors were chosen to contrast birds from nests and do not depict natural colors. Illustration by DMP.

into account in order to understand function (Zyskowski and Prum, 1999; Hall et al., 2013; Medina, 2019).

Nest Shape

There is general agreement on the categories of classification for overall nest shape (open cup, dome, cavity; **Figure 1**), and these groupings have been widely used (Price and Griffith, 2017; Duursma et al., 2018; Fang et al., 2018). Broadly, nests can be classified as open cups and domes—those that have a roof. There are also cavity nests, which may or not contain an open cup or a dome within. Some nest shapes are hard to classify, like the pouches of some weavers, that are so deep that they are effectively more similar to a domed nest than an open nest of any kind. Similarly, the nests of some galliforms (like bush-turkey or malleefowl) are not conventional domed nests (with a roof and side entrance) but are, instead, large mounds on the ground where eggs are buried (Hansell, 2000).

Nest shape has often been considered as an important taxonomic character that is ideal for mapping onto phylogenies for the purposes of ancestral reconstruction (Winkler and Sheldon, 1993; Zyskowski and Prum, 1999). This is because nest shape is considered to be invariable within families and genera, but variable at higher taxonomic levels (Price and Griffith, 2017; Fang et al., 2018; Medina, 2019). Hansell (2000) highlights, however, that some families have species with nests that are cup, domed and in cavities (e.g., Furnariidae, Thraupidae, Psittacidae). Parrots for example, are known for using cavities, but there are a handful of species that do not (e.g., *Myopsitta monachus*, domed nest).

Nest Size

Besides the general shape, another trait considered part of the morphology of a nest is its size. Many studies use length and width to describe nest size (Heenan and Seymour, 2011; Windsor et al., 2013; Lambrechts et al., 2017), although in the case of domed and cavity nests, width is harder to measure, and width is more often used as a measure for open nests (referred to as inner cup width). Other measures related to nest size that can be useful in describing the general structure of the nest are the cup depth, width of the walls and the thickness of the base.

Unlike general nest shape that is highly conserved across and within species, nest size is much more labile. There is considerable variation in nest size across species, and the main predictor of nest size is the body size of the builder (Slagsvold, 1989; Møller, 2005; Deeming, 2013). However, within individuals there is also significant variation in the nest size. African weavers (*Ploceus* spp.) build multiple nests during the breeding season and individuals can change the size of their nests over time, suggesting considerable plasticity in this trait, which in fact could be related to changing weather across the season (Walsh et al., 2010, 2011). It is important to consider that African weavers use nest building as part of courtship, so like other phenotypic traits, nest size may be driven by multiple selective pressures, including sexual selection (Soler et al., 1998; Møller, 2005; Moreno, 2012; Tomás et al., 2013). Although only affecting species where nests are sexually selected, if multiple selective forces shape the size of the nest, the potential to respond to climatic conditions might be constrained. Indeed, both sexual and natural selection can drive the evolution of nest size in the same direction (e.g., toward larger size), making it difficult to tease apart the contributing roles of drivers of trait variation. A similar example of concurring selection pressures involves female penduline tits (*Remiz pendulinus*), which face high energetic demands during incubation and, thus, select a mate based on the insulation capacity of the nest he constructs (Hoi et al., 1994).

Nest Lining and Composition

Another component that will be crucial in our discussion of the links between nests and climate is the lining of the nest. Many birds (but not all) collect feathers, plant down, and/or fur and use them to cover the inner cup, which is thought to be critical in providing insulation. Materials are classified as lining if they have no structural function and are placed within the nest (Hansell, 2000; Mainwaring et al., 2016). This trait is usually quantified by the amount (weight) of lining inside a nest (Mainwaring et al., 2012), but the type of materials used is also important as both are crucial in understanding the thermal efficiency of the nest as a whole. Materials used in nest building are highly variable and can range from mud and saliva in rufous hornero (*Furnarius rufus*) and swift (*Aerodramus fuciphagus*) nests, to paper money and bones in raptor nests (Hansell, 2000; Ellis et al., 2009). Thus, when analyzing other nest characteristics, such as mass, it is important to take component materials, and their physical density, into account.

Birds are selective in choosing materials for their nests, which suggests adaptive value in this behavior (Bailey et al., 2014; Muth and Healy, 2014; Briggs and Mainwaring, 2019). The choice of material can be relatively consistent within species (Biddle et al., 2018a). Pied flycatchers (*Ficedula hypoleuca*) prefer deer fur over other materials (Briggs and Mainwaring, 2019), and zebra finches (*Taeniopygia guttata*) choose materials based on size and structural properties (Muth and Healy, 2014). Considerable variation across closely related species is also observed. The magpie lark (*Grallina cyanoleuca*) and its sister species the torrent-lark (*Grallina bruijnii*) build a cup nest made of mud, but most members of the family (Monarchidae) weave their nests from plant material (Del Hoyo et al., 2017). Indeed, birds can show flexibility in selection of materials observed within species and across very small spatial scales (up to 4 km) (pied flycatchers, Briggs and Deeming, 2016). Parents actively adjust nest building decisions to match the availability of local materials, such that urban populations of multiple species have been shown to incorporate man-made materials (Wang et al., 2009; Suárez-Rodríguez et al., 2013). Thus, unlike other traits like nest shape, the choice (and amount) of nest materials seems to have great evolutionary potential to respond to selective pressures.

The thermal performance and structural properties of the materials used for nest construction are of primary importance, and the way materials are laid down is critical in changing air flow and water absorption thereby influencing insulation capacity (Skowron and Kern, 1980; Rohwer and Law, 2010; Crossman et al., 2011; Deeming and Biddle, 2015; Biddle et al., 2018b,c). However, the choice of nest materials is also associated with factors other than thermal properties that, in combination, enhance breeding success. Males often select nest materials to increase nest appearance and thus his attractiveness, or can also use materials that have anti-parasite benefits (Veiga et al., 2006; Mennerat et al., 2009). The spotless starling uses unpigmented feathers and aromatic plants to enhance antimicrobial protection and nestling survival (Ruiz-Castellano et al., 2018). The European starling adds aromatic herbs to their nests that improve nestling condition through stimulating higher parent attendance and longer incubation bouts (Gwinner et al., 2018).

NEST MORPHOLOGY AND CLIMATE

Nest Shape

Among species that build a nest structure, the presence or absence of a roof, or whether or not, it is placed in a cavity, can have large effects on the thermal performance (Griffith et al., 2016), leading to the expectation of intraspecific variation in nest shape in species with wide geographic ranges. It is puzzling that within-species, the potential to dramatically alter nest shape (e.g., from cup to domed or vice versa) appears to be rare (Cardoni et al., 2017). It is possible that general nest shape is already well adapted to environmental conditions in the species' current distribution, such that variation at this level is unnecessary at smaller taxonomic scales. Alternatively, changing nest shape could require high levels of flexibility in building behaviors, which might be difficult to develop. Although very rare, there are examples of variation in nest shape within species. One example is the golden-headed cisticola (*Cisticola exilis*), which is described as having open cup nests in some parts of its distribution in NE India and domed nests in other parts (Del Hoyo et al., 2017), but the causes for these differences are unknown. Another interesting case is that of the bay-capped wren-spinetail (*Spartonoica maluroides*), which builds two different nest types in the same region in Argentina, but the causes for such variation are not completely clear either (Cardoni et al., 2017). These systems might be ideal to investigate the role of climate in driving intraspecific nest variation at broader scales. Current information, however, is not enough to draw any conclusions, and climate is not the sole selective pressure acting on nest shape. For example, weavers, which have domed nests, are heavily parasitized by cuckoos in Africa and their domed nests have been suggested to decrease parasitism rates (Krüger and Davies, 2004; Medina et al., 2020).

Nest shape can play an important role in extreme environments where suboptimal nest design can be lethal to the offspring. The zebra finch, for example, faces high temperatures during the breeding season in Australia, and there is some evidence that by constructing domed nests parents can protect the eggs from direct sunlight which may reduce the risk of eggs reaching lethal temperatures (Griffith et al., 2016). Indeed, looking at the interspecific level some recent studies have suggested that domed nests might be a type of specialization in arid environments. Duursma et al. (2018) found that in Australia, arid places have a higher frequency of domed nest species compared to other non-arid regions. Conversely, Medina (2019) did not find associations between nest shape and particular environments in Australian species, but evidence that species with domed nests have smaller distributions and suggested that dome nests were lost as birds expanded to other environments and the range of climatic conditions. Nevertheless, these findings remain to be rigorously tested worldwide, through broad comparative studies that take into account phylogenetic, and spatial correlations.

Overall, explanations for the evolution of nest shape in passerine birds have focused on two main hypotheses: predation pressure versus microclimate variation (Martin et al., 2017). According to a long-standing assumption, domed nests are more common in tropical and southern hemisphere regions because the shape of the dome reduces predation risk (Oniki, 1979). However, studies have recently revealed that predation rates are similar for different nest types (cup and dome) and across latitudes (Martin et al., 2017; Mouton and Martin, 2019), and birds seem to respond to predation risk by changing nest placement rather than nest shape (Forstmeier and Weiss, 2004; Peluc et al., 2008). In fact, domed nests are associated with smaller absolute body size in passerines, supporting thermoregulatory explanations for their evolution (Martin et al., 2017). Smaller individuals have higher rates of heat exchange due to their disproportionately large surface area to volume ratios compared with larger-bodied individuals, with consequences for energy and water budgets at both ends of the temperature scale (hot and cold conditions) (Boyles et al., 2011). Domed nests that confer a stable microclimate, with protection from temperature extremes, rainfall and sun exposure, may reduce the thermoregulatory costs of attending parents and provide thermal benefits for embryos and nestlings. Such benefits may lead to a reduction in parental effort, increased offspring growth rates and reductions in the lengths of the incubation and nestling periods, thereby reducing predation risk, with disproportionate effects for smaller species (Martin et al., 2017; Matysiokov and Remes, 2018).

In summary, studies have pointed to considerably low intraspecific variability in nest shape, and species with such variation are still poorly investigated. Under the broad interspecific level, however, nest shape may represent an important adaptation to the selective pressures of the environment with dome nests commonly occurring in small ranges and arid places (Duursma et al., 2018; Medina, 2019). Studies have also demonstrated associations between dome nests and body size highlighting the thermal function of these structures, although further research is still required to fully dissociate climate-related hypotheses from predation risk (Martin et al., 2017; Medina, 2019). Future research testing for associations between nest shape (e.g., domed versus cup), passerine body size and the nature and extent of weather extremes, both hot and cold, may improve our understanding of the direct effects of weather on nest microclimate versus body size-related thermoregulatory costs.

Nest Size

Traditionally, large nests are thought to be adaptive in cooler regions where they can confer a more stable microclimate than smaller nests (Collias and Collias, 1984) and, thus, climate-driven selection pressures on nest size are likely to be pronounced. Variation in nest size is more extensively investigated at the intraspecific level across large geographic ranges with distinct environmental conditions or in relation to the length of breeding seasons where large shifts in weather are observed across months. For instance, the ring ouzel (*Turdus torquatus*) is widely distributed in Eurasia, including across elevations, such as in the montane regions of West Carpathians, Slovakia (Janinga and Višòovská, 2004). Variation in nest width and depth in this species is correlated with differences in the climate (wider and deeper nests are found in cooler climates), a result of either latitude or elevation gradients (Janinga and Višòovská, 2004). The yellow warbler (*Dendroica petechia*) shows even more pronounced building modifications, whose distribution extends to subarctic climate where they build larger, thicker, taller cup nests that are also less porous and more insulated than nests from warmer regions (Rohwer and Law, 2010).

Although there is a good deal of correlational evidence for a link between nest size and local climate, studies need to apply scrutiny in assigning causal mechanisms and consider additional factors that are potentially important in the interplay between climate and nest size (or morphology in general). For example, in the black-throated blue warblers (*Setophaga caerulescens*), nest wall thickness increases with elevation where temperatures are generally lower. Yet, there is no relationship between wall thickness and ambient temperature during the breeding season (Smith et al., 2018) and further studies are needed to understand the real extent of temperature in driving differences in nest size across elevation in the species. Likewise, the bearded reedling (*Panurus biarmicus*) builds larger and thicker cup nests when facing lower daily minimum temperatures, but nest height and the shape of the base are influenced mostly by the density of reeds, as these birds adapt their nests to the structure of the supporting vegetation (Malzer and Hansell, 2017). The cavity nester, thorn-tailed rayadito (*Aphrastura spinicauda*) builds smaller nests in warmer months as a consequence of using less insulating material (Botero-Delgadillo et al., 2017). However, a smaller nest size is not necessarily the result of selection for cooler nests in warmer temperatures, as time constraints on breeding later in the season might cause parents to accelerate the nest building process, or nest material might simply become scarce, thereby affecting nest morphology (Botero-Delgadillo et al., 2017). In a similar example, the wood thrush (*Hylocichla musteline*), builds shorter, shallower and thinner open cup nests as the season progresses and temperatures increase (Powell and Rangen, 2000). However, the increasing energetic constraints parents face as the season advances could also cause a reduction in building effort over time. Additionally, bigger nests might be more exposed to predators later in the season when leaf-out occurs, suggesting variation in nest construction may be driven by changing predation pressure (Powell and Rangen, 2000).

Indeed, selection for larger nests could be constrained by predation risk, since many predators are diurnal and use vision to locate nests, and it is known that bigger nests, relative to body size, are more susceptible to predation (Møller, 1990; Martin and Li, 1992; Biancucci and Martin, 2010; Mouton and Martin, 2019). In fact, the pressure to construct small and inconspicuous nests may outweigh the pressure to produce a suitable nest microclimate (Møller, 1990; Crossman et al., 2011, but see Akresh et al., 2017; Kubelka et al., 2019). These competing selection pressures can be particularly important for exposed, open cup nesters (Matysiokov and Remes, 2018). If competing pressures constrain the evolution of thermally adapted structures, parents might compensate for the thermal deficiencies of smaller nests by spending more time incubating or covering the clutch with leaves to regulate the temperature and relative humidity, although the latter strategy can also be employed to camouflage the clutch (Collias and Collias, 1984; Kreisinger and Albrecht, 2008; Prokop and Trnka, 2011). However, supposing that parents instead build thicker walls and base, the resulting reduction in the area of the inner cup could limit clutch or egg size (Suárez et al., 2005), and parents would face a trade-off between predation avoidance and offspring production. Although it is also possible that smaller nests have denser walls or that nest size (cup space) is not linked to clutch size (Antonov, 2004; Biancucci and Martin, 2010; Akresh et al., 2017; Malzer and Hansell, 2017). Collating data on nest dimensions and density for a wide range of species from distinct climatic regions and predator regimes would be key to further our understanding on this system by testing two inter-related questions: could predation and thermal selection pressures on open nests lead to lower offspring production?; and would a decrease in size be compensated by material choice and wall density?

The evidence presents a tight link between nest size and thermal properties of the nest, but structural support might be a very important pressure as well. An investigation with cup nest from 36 Australian species revealed that as species body size increases, nest surface area increases isometrically, but nest wall thickness increases on a higher scale than would be expected isometrically or if nests were built to prevent heat loss (Heenan and Seymour, 2011). This result led the authors to conclude that structural support was the most fundamental selective pressure driving the evolution in nest size among cup nesters (Heenan and Seymour, 2011). However, this study did not look into the relationships between nest morphology and the environment, and a later investigation using the same species revealed that nest insulation is in fact highly correlated with local climate (Heenan et al., 2015). Thicker nest base and better insulating materials, such as wool and feathers, are used by different species in cool climates and thinner nest base and poorly insulating materials, such as sticks and grasses, in warm climates. This trend is more pronounced when accounting for humidity, where species from warm climates facing high precipitation build nests that are poorly insulated and consequently less absorptive (better draining). Authors concluded that nest material, more than nest size, is the central element varying with climate across Australian cup nesting species (Heenan et al., 2015).

Unlike nest shape, nest size shows considerably high variation both within and between species. The variety of nest sizes seems to match the constraints of local and temporal climate conditions, where larger structures are built in cooler environments. From a macroevolutionary perspective, size seems to correlate with climate where nests with denser walls and thicker base are found in cooler and drier regions (Heenan et al., 2015). However, a clear trend is not always detected as many interplaying factors seem to drive nest shape (Kern et al., 1993; Biancucci and Martin, 2010) and further studies including phylogenetic comparisons a global sample of species are needed to reach a thorough understanding of these findings.

Nest Lining and Composition

Nest lining can comprise a large part of the total nest mass and is among the most flexible of nest traits (McGowan et al., 2004). In particular, species that face changing weather conditions throughout the months (e.g., those with long breeding seasons in temperate regions), show large variation in the composition and amount of nest lining (Mainwaring and Hartley, 2008; Akresh et al., 2017). For example, in cavity nesters, the amount of animal hair in collared flycatcher nests and the diversity of animal hair in great tit and blue tit nests decreases as the breeding season advances. This suggests that the insulating properties of fur are no longer necessary as ambient temperatures increase (Harnièárová and Adamík, 2016).

Seasonal change in the composition and amount of lining, however, can be a by-product of material availability. The preference for animal hair early in the season may reflect low availability of plant and other nest materials (Harnièárová and Adamík, 2016). In the blue tit, the mass of nest lining also declines with the season as ambient temperatures increase. Authors suggest that the decrease in lining is adaptative, rather than a reflection of availability, because nest base mass remains constant over the season (Mainwaring and Hartley, 2008). Similarly, in long-tailed tits, a dome nesting species, seasonal decline in nest lining mass could be attributed to changes in resource availability. However, by supplying feathers to breeding pairs, McGowan et al. (2004) confirmed that parents incorporate lining material in a manner that matched insulating properties with local temperature.

Besides variation in nest lining and materials within individuals through the season, there is also regional variation in the types of materials used in nest construction. Populations from the same species that inhabit different regions choose materials depending on regional availability (Clark, 1991; Suárez-Rodríguez et al., 2013). Nest composition is the central factor for nest microclimate in the mound nest of the Australian bush-turkey. Males build mounds of leaf litter on the ground and the balance between the amount of material, water and sufficient mixing provides the appropriate temperature through microbial heat generation. Mounds can self-generate heat for up to several weeks and it is known that in higher latitudes the rate of decomposition is lower than in lower latitudes. Curiously, this is directly due to material composition, and male bush-turkeys have to compensate for the low rate of decomposition of plant species in higher latitudes by using more material (Seymour and Bradford, 1992). The common amakihi (*Hemignathus virens virens*) is distributed across a range of elevations in the islands of Hawaii with distinct vegetation communities and climatic conditions. The environmental breadth across this species range led to high variation in nest morphology, which was associated with successful breeding under varying environmental conditions. The common amakihi adjusts insulation by changing composition in elevated areas with cold, dry conditions compared with low wetland areas with extremely hot, wet conditions (van Riper, 1980; Kern and Van Riper, 1984). In addition, nests in warmer areas are built higher in the canopy and closer to the tree's trunk, while in cooler areas, nests are placed near the edge of the canopy, possibly to optimize exposure to sunlight (Kern and Van Riper, 1984). Furthermore, this example provides evidence that nest material as well as placement have a combined role in conferring a suitable microclimate (Horvath, 1964; Kern and Van Riper, 1984). The tight link between habitat and nest building shows the importance of habitat conservation and the availability of nest materials and nesting locations. Such impacts should test a species' ability to adaptively respond by changing its nest morphology to conform to the newly imposed conditions (Martin, 2014).

In summary, similarly to nest size, there is considerable variation in nest composition within and between species. In support to the climate adaptation hypothesis, less insulating material is used in lower latitudes and altitudes, but a stronger pattern is observed with the advancement of breeding season and a consequent increase in temperature (e.g., Mainwaring and Hartley, 2008; Deeming et al., 2012). Yet, we still observe high building variability specially across locations (**Supplementary Table 2**) evidencing that alternative selective pressures, such the availability of nest materials, represent constraints to nest lining and composition. In particular, the level of habitat conservation has a direct impact on material availability and broad scale studies testing species' ability to adaptively respond to environmental degradation by changing nest construction should reveal interesting patterns on how species conform to unfamiliar and unexpected conditions and if that hampers building adaptation to climate conditions (Martin, 2014).

FUTURE DIRECTIONS

We highlight that many of the examples identified in this review are correlative and, so, causal relationships have only been inferred. Thus, it is important to exert caution when drawing conclusions about factors underlying nest building flexibility, as multiple factors can influence nest building behavior and morphology. We have identified several of these, including predation pressure, anti-parasite benefits, sexual selection, other parental strategies, availability of nest material and time constraints. In addition, a paucity of phylogenetic breadth in investigations of nest building behavior also points to a wide gap in our knowledge of the evolution of nest morphology. In particular, although also correlative, broad phylogenetic scales can provide an evolutionary perspective about the broad and global correlates of climate and nest morphology. Here we point to research directions that, to date, have received insufficient or no attention, and if explored with experiments or on a macroevolutionary scale, will be crucial in further elucidating a comprehensive understanding of nest building behavior evolution.

As we show during this review, humidity seems to strongly influence nest construction behavior (Heenan et al., 2015), although, most studies of nest microclimate primarily consider the effect of temperature (73%, **Supplementary Table 1**). Recent advances in our understanding of thermal physiology suggest that humidity may have consequences for chick growth and parental body condition via increasing the costs of thermoregulation; high humidity reduces the gradient driving evaporation thereby reducing the rate of heat loss via evaporative cooling, with potential to compromise energy and water budgets (Gerson et al., 2014). This may be particularly important in the tropics where high humidity coincides with high temperatures, and evaporative cooling via panting is the primary means by which passerines dissipate excess body heat. Comparing the morphology and microclimates of nests of tropical species with those from other climate zones may provide greater insights into how weather as a whole, rather than simply temperature, shapes the evolution of nest morphology.

Another important factor that deserves careful consideration when investigating climate-related selection pressures on nest morphology is the embryo physiology. Altricial and precocial species have different thermoregulatory capacities early in life (DuRant et al., 2013b), which may pose distinct nest microclimate demands. Precocial species possess an early capacity to maintain body temperatures, as they are quite mature at hatching when they may not depend on nest microclimate anymore. Much of the energy in precocial chicks is, therefore, allocated to thermoregulation and, as a consequence, these birds grow at slower rates. Conversely, altricial nestlings grow at higher rates, but depend on nest microclimate and parental care to maintain optimal body temperatures (Tortosa and Villafuerte, 1999). In that way, nest insulation could be highly crucial for altricial species until they reach an age where they present effective endothermy. These two types of embryo development are likely to have been important in driving the evolution of nest morphology and positioning, because maintaining an adequate environment for nestlings could lead to stronger pressures in altricial species (DuRant et al., 2013b). This idea has not been tested before, but many Paleognaths like emus and other precocial species have minimal nests or lack any type of nest structure. Alternatively, given the fast embryonic development in precocial species, it is also possible that nest microclimate is equally or more important to these species, or that they possess high levels of embryonic resistance (Fu et al., 2017). Phylogenetic comparative studies on nest morphology are needed, including non-passerine species—which are mostly precocial—because they will have the potential to reveal which nest traits are essential for chick development. Comparing the structure and microclimates of nests of species with different developmental modes may provide insights into which traits of nest morphology are important for incubation and which others are important for chick development and protection.

CONCLUSION

We have shown that variation in climate conditions across space (latitudinal and altitudinal gradients) and over timescales (years and breeding season) are important drivers of nest building behavior. We have provided multiple examples of how variation in nest morphology can be explained as an adaptive response to climatic variation, although many studies are correlative. Nest shape, and to a lesser extent, nest size, lining and composition are components of nest morphology that are heritable and phylogenetically conserved (Møller, 2005; Heenan et al., 2015; Price and Griffith, 2017; Fang et al., 2018; Medina, 2019). This conservatism would primarily indicate relative resistance to selective pressures. However, high phylogenetic signal may generally reflect that building behavior interacts with evolutionary pressures of species local climate under a large macroevolutionary scale (Heenan et al., 2015; Price and Griffith, 2017; Medina, 2019). In particular, nest composition has been pointed as the central component responding to climatic selective drivers, as insulation is higher in low ambient temperature and humidity (Skowron and Kern, 1980; Heenan and Seymour, 2011; Heenan et al., 2015). Parallelly, at the intraspecific level, nest shape is markedly less labile than the remaining features of nest morphology revealing that it is likely less subject to selection. As a consequence, we observe a considerably higher number of studies investigating adaptations in size, lining and composition within species, all traits that seem correlated (92%, **Supplementary Table 1**). We have observed that species generally tend to converge on similar solutions for nest design under similar environmental conditions, although a clear trend cannot be conclusively drawn (**Supplementary Tables 1, 2**). Nests tend to be bigger and contain more material in higher latitudes and elevations (61% of studies) but mostly so early in breeding seasons (76% of studies; **Supplementary Tables 1, 2**). These adaptations are most commonly driven by low temperatures where bigger diameters, thicker walls, deeper inner cups and more insulating materials confer protection against heat loss, although the local ambient humidity is also crucial in determining if nests will be thicker and more insulated (**Supplementary Tables 1, 2**).

More studies of nest morphology, with broad global representation and larger temporal scales, will provide greater understanding of how, and to what extent, climatic variation shapes nest morphology and provide insight into whether birds can adaptively respond to rapid changes in contemporary climate (Mainwaring, 2015). Our review provides strong evidence for links between nest morphology and climatic variation, suggesting that nest building behavior can respond to temporal changes in contemporary climate. Indeed, a recent study showed that Goshawks in Denmark have been responding to rising spring temperatures over the past several decades (1977–2014) by increasing nest size (Møller and Nielsen, 2015). However, whether such shifts will be sufficient to track changing climate remains in question and requires greater understanding of whether adaptation will require evolutionary, genetic change in nest construction behavior or can be achieved via plasticity in existing behavior (Møller, 2005). Our review details high levels of plasticity in nest building behavior associated with particular nest traits (e.g., nest size and composition are more flexible than nest shape) but more research is needed on the genetic basis of these behaviors, if we are to improve our capacity to predict species' responses to ongoing climate change.

AUTHOR CONTRIBUTIONS

DMP and IM designed the study. DMP, JLG, and IM performed the bibliographic research and prepared the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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REVIEW
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The Effects of Weather on Avian Growth and Implications for Adaptation to Climate Change

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Climate change is forecasted to generate a range of evolutionary changes and plastic responses. One important aspect of avian responses to climate change is how weather conditions may change nestling growth and development. Early life growth is sensitive to environmental effects and can potentially have long-lasting effects on adult phenotypes and fitness. A detailed understanding of both how and when weather conditions affect the entire growth trajectory of a nestling may help predict population changes in phenotypes and demography under climate change. This review covers three main topics on the impacts of weather variation (air temperature, rainfall, wind speed, solar radiation) on nestling growth. Firstly, we highlight why understanding the effects of weather on nestling growth might be important in understanding adaptation to, and population persistence in, environments altered by climate change. Secondly, we review the documented effects of weather variation on nestling growth curves. We investigate both altricial and precocial species, but we find a limited number of studies on precocial species in the wild. Increasing temperatures and rainfall have mixed effects on nestling growth, while increasing windspeeds tend to have negative impacts on the growth rate of open cup nesting species. Thirdly, we discuss how weather variation might affect the evolution of nestling growth traits and suggest that more estimates of the inheritance of and selection acting on growth traits in natural settings are needed to make evolutionary predictions. We suggest that predictions will be improved by considering concurrently changing selection pressures like urbanization. The importance of adaptive plastic or evolutionary changes in growth may depend on where a species or population is located geographically and the species' life-history. Detailed characterization of the effects of weather on growth patterns will help answer whether variation in avian growth frequently plays a role in adaption to climate change.

Keywords: environmental change, development, heritability, life-history, maternal effects, natural selection, plasticity

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INTRODUCTION

Avian growth can affect fledgling survival and recruitment, and early life experiences are known to impact adult phenotypes (Haywood and Perrins, 1992; Lindström, 1999; Maness and Anderson, 2013; Merrill and Grindstaff, 2018). Given gradual warming and increasingly stochastic weather conditions under climate change, some growth strategies might result in higher fitness than others.

Therefore, predicting future changes in fitness and demography under climate change could depend on understanding the effects of current weather variation on offspring growth. The consequences of weather variation on offspring development will likely be complex and will, to some degree, depend on a species' life-history and ecological niche.

Growth patterns in birds vary, and differences among populations may be adaptations to their local environments (Ricklefs, 1968; Emlen et al., 1991; Starck and Ricklefs, 1998). Global patterns of variation in avian growth within species can generate hypotheses for how the changing climate will influence growth-related traits. For example, given the observation that individuals tend to be smaller in warmer habitats both within and across species (Bergmann's Rule; Bergmann, 1847 as cited in Salewski and Watt, 2017) we might predict that for a given species, natural selection will favor nestlings that fledge at a smaller size in a warmer climate (Millien et al., 2006). Introduced House Sparrows *Passer domesticus* in North America and Australia both exemplify predictions from Bergmann's rule: birds in the colder regions of both continents are on average larger (Johnston and Selander, 1964, 1973; Andrew et al., 2018). Clines in body size could be driven by natural selection developmental constraints, or both (Fleischer and Johnston, 1984; Andrew et al., 2018). Effects on size during development are important because many bird species approach their final structural size before fledging, meaning there may be little opportunity for compensation later in life (Gill and Prum, 2019).

Plastic adjustment of growth could allow rapid adaptation to changing conditions, but evolution of growth traits might be required if current environmental cues no longer predict future environments. To predict possible phenotypic changes in nestling growth we need to understand how weather variation affects nestling growth, how new weather conditions under climate change are changing the selection on avian growth traits, and the additive genetic and environmental variance of growth traits. Some studies have identified carry-over effects of growth on adult fitness with negative and positive consequences for body size (Gardner et al., 2011; Teplitsky and Millien, 2014; van Gils et al., 2016), but few studies examine whether patterns in growth are adaptive or maladaptive. Examining growth-environment relationships jointly with patterns of genetic change is important because phenotypic plasticity can mask evolutionary change (Merilä et al., 2001; Bonnet et al., 2017; Dobson et al., 2017), and plastic responses can contribute to an adaptive or maladaptive response to changing weather conditions (Ghalambor et al., 2007; Snell-Rood et al., 2018). An essential aspect of studying growth is to quantify it in a way that allows among population, individual and genetic variation to be estimated (**Box 1**).

In this review, we (1) highlight why studying weather-related changes in avian growth might be important to understand avian responses to climate change, (2) review the currently documented effects of weather on avian growth in wild populations, and (3) highlight that understanding the selection operating on growth traits and the inheritance of growth traits is needed to predict future phenotypic responses. We define weather as local within-year variation in temperature (of air and sea surface), solar radiation, precipitation and wind, and climate as the average weather across multiple years for a given region. We explore the effects of minimum, maximum, average, and duration (heatwaves, rainfall) of weather variables.

IMPORTANCE OF STUDYING WEATHER-RELATED CHANGES IN AVIAN GROWTH

Understanding weather-related changes in avian growth is important for two reasons: some individuals or genotypes might survive better than others in stressful weather conditions, and weather variation may change a population's demography through influences on nestling traits.

Plasticity of Avian Growth and Development

Because of genetic, environment, or parental effects individuals will differ in their growth. Understanding the causes of these growth differences is important because some individuals may have higher fitness under changing conditions (Kruuk, 2004; Wilson et al., 2010). In theory, the same individual or genotype could also produce several different phenotypes given different weather conditions (phenotypic plasticity), and the plasticity of an individual's phenotype could also vary among individuals because of genetic, permanent environment, or parental effects. Plastic changes have gained recognition as common responses to changing environmental conditions (Ghalambor et al., 2007; Charmantier and Gienapp, 2014; Snell-Rood et al., 2018). Central questions in evolutionary ecology are (1) whether plasticity will allow adaptation to new weather conditions, and (2) how plasticity might affect the rate of evolutionary change.

Studying the plasticity of avian growth requires the estimation of how growth patterns can change for a given individual (or a given genotype) across different environments. Such measures are impossible at the individual-level because a bird only grows once. However, in long-lived and philopatric species, associations between growth and weather variation may be likely to result from plastic rather than evolutionary responses because the population genetic background may change little from 1 year to another. In a wild setting, a cross-fostering experiment across a weather gradient (experimental or natural) may reveal if different families have on average different or similar growth patterns across environments (for a discussion on artificial breeding designs, see Roff and Wilson, 2014). To our knowledge, no studies have analyzed cross-fostering in wild birds, with the goal of measuring differences among families in changes in growth patterns across weather gradients.

Because a proportion of the variation in growth traits are determined by parental behavior we might be able to measure the plasticity of nestling growth by considering nestling growth traits as parental traits in species where faithful pairs repeatedly reproduce (Lloyd and Martin, 2004; Wilson et al., 2005). Nestling growth traits that are measured across years for parents can then be considered repeated

BOX 1 | Methods for quantifying growth.

Avian growth can be investigated using a broad range of traits and different statistical modeling approaches. Often, measurements of size or shape near fledging are used because these are more comparable across studies and can predict post-fledging survival (Maness and Anderson, 2013). However, single time point measurements can hide variation in growth among individuals if individuals follow different trajectories to the same final size (**Figure 1**).

Repeated measurements made throughout nestling development can be used to fit a curve to the data as a function of age. For growth data, logistic models are often used, and the model's **asymptote**, **maximum relative growth rate**, and **timing of maximum growth** may be estimated as biological parameters of interest describing growth (**Figures 1**, **2A**; Tjørve and Tjørve, 2010; Aldredge, 2016). The unified family of growth models proposed by Tjørve and Tjørve (2010, 2017) allows flexible, comparable, and biologically interpretable estimates from various growth model families. Biologically, the **asymptote** should provide an estimate of the maximum size reached by a nestling. However, the **asymptote** in many models may not be a good indication of a nestling's fledging mass, as a nestling could fledge before the maximum mass is reached, or in some avian species nestlings reach an asymptote and then decline in mass before fledging.

Such *function-valued trait approaches* summarize the growth trajectory and enable researchers to explore whether different environments affect the growth rate, timing, or size of a nestling. Linear and polynomial functions could also be used, with the terms of the polynomial being treated as the parameters of interest. Instead of fitting functions to a growth trajectory, sometimes the average difference between consecutive daily measurements (e.g., Peck et al., 2004; Harter, 2007; Divoky et al., 2015) or the daily deviation from growth in ideal conditions are used as an indication of daily growth (Keller and Noordwijk, 1993).

Character-state models provide a flexible method for modeling growth, where one can estimate age-specific measurements as separate, yet correlated traits (Roff and Wilson, 2014; **Figure 2B**). Note that character-state and polynomial functions are equivalent in many situations. In a character-state approach covariances among age-specific masses can be fitted across all ages, or be restricted to consecutive ages only, in what is called an "ante-dependence" model (see the supplementary material of Hadfield et al., 2013; Thomson et al., 2017; Hadfield, 2019). Both function-valued trait and character state approaches to modeling growth are identical to models that measure trait plasticity across environments, but replace environmental variation with age (Falconer, 1952; Via and Lande, 1985; Jong, 1990; Gavrilets and Scheiner, 1993; Chevin et al., 2013). Function-valued trait approaches can perform poorly if individuals or genotypes have different curve shapes and can be harder to interpret biologically (Roff and Wilson, 2014). Generally, function-valued trait approaches use fewer parameters. Therefore, when sufficient data are available, comparison of function-valued and character-state approaches might be valuable in determining when during ontogeny function-valued trait approaches are not capturing variation during growth (Morrissey and Liefting, 2016). If a linear model is used, environmental effects on the slope or intercept of the line could be detected, yet a gain or loss of mass at any specific time during growth, which could be biologically important, would be difficult or impossible to detect. A character-state might be better able to determine *when* during ontogeny the environment affects a trait. Houslay (2017) provides accessible tutorials implemented in the R package MCMCglmm for both character state and function-valued trait approaches that could be used to model avian growth (Hadfield, 2010). Function-valued trait and character-state approaches can be analyzed in a mixed model framework, so that hierarchical (co)variances are estimated (function-valued trait approach, Aldredge, 2016; character-state approach, Thomson et al., 2017). Further, Bayesian models now allow the fitting of flexible models that can estimate the fixed effects of weather and environmental variation on specific parameters or age-specific traits in a single model (Hadfield, 2010; Bürkner, 2017).

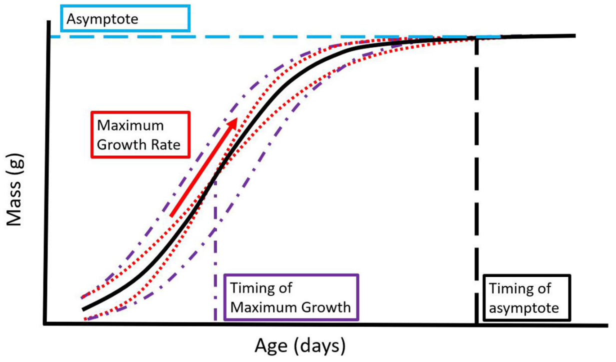

FIGURE 1 | Parameters estimated in a standard logistic curve. The maximum growth rate (red arrow) gives an indication of the speed of growth, the asymptote gives an indication of the nestlings' maximum size achieved during the period of study (blue horizontal dash), the timing of maximum growth gives an indication of when during ontogeny maximum growth occurs (purple/vertical dash + dotted line), and the timing of the asymptote might indicate developmental timing (black vertical dashed line). Five growth curves are shown, with the same asymptote but varying in the timing of maximum growth (purple dash and dotted lines) or in maximum growth rate (red dotted lines). All curves have the same asymptote as the reference curve (thick black curve) but vary in their trajectory. If a study of nestling growth only measures mass at the asymptote as in this example, variation throughout the trajectory of the growth curve is hidden. Whether this variation impacts fitness is currently unknown.

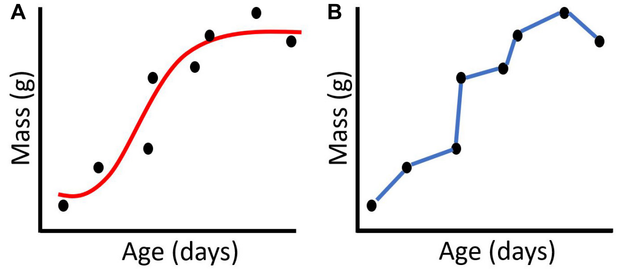

FIGURE 2 | Hypothetical example of a **(A)** function-valued trait approach and a **(B)** character-state approach for modeling a chick growth curve.

measures of a parental trait. We can then try to examine the plasticity of the parental care contribution to nestling growth by examining how nestling growth traits vary across environments for a given parent or pair of parents. Importantly, because reproductive investment is a complex function of age and parental condition, such a model will require careful consideration of parental age or breeding experience (McCleery et al., 2008) and the weather conditions parents experience. Consequently, informing such a model will likely require large sample sizes but will provide valuable information on the suite of growth responses individual parents or parental genotypes could generate.

One of the challenges in studying plastic responses in wild populations is determining the environmental variable to which an organism responds (Scheiner, 1993; Gienapp and Brommer, 2014). This problem is further complicated because a trait could be affected by multiple weather variables, interacting weather variables, or even the same weather variables in different ways at different times throughout ontogeny (**Figure 3**). Recent statistical techniques try to address the difficulty of identifying time windows of weather variation that affect a trait of interest (van de Pol et al., 2016). The van de Pol et al. (2016) method is an exploratory approach that compares multiple windows within a period of time (relative to the biological variable or an absolute time frame) to determine those that best predict (relative to all windows examined) the trait of interest. To understand when during the breeding season weather affects nestling growth, it may be useful to explore weather variation within the prelaying, prenatal, and growth stages (**Figure 3**). Importantly, we mainly discuss physical growth in this review, but many of the impacts of weather also affect the development (e.g., cognition, thermoregulation, motor function) of nestlings. Understanding how and when during the breeding season development is affected by weather is an additional complexity that will be important to study for a more complete understanding of the impacts of weather.

In the context of growth and development, identifying environmental correlates may still be challenging because weather variation among prelaying, prenatal, and postnatal periods might be tightly correlated – making it difficult to disentangle during which period weather variation affects a trait. For more easily manipulated weather effects like temperature, experimental work may allow researchers to measure the effects of different time windows by manipulating temperature during specific time periods (Andrew et al., 2017; Andreasson et al., 2018, 2020a; **Figure 3**). Exploring effects of weather variation outside the breeding season will be valuable if weather patterns are expected to have long-term effects on the resources available or the condition of parents during the breeding season. Understanding the environmental cues that affect the expression of a character is essential because plasticity might allow persistence in the face of changing weather conditions (Vedder et al., 2013), but could also increase the speed of extinction if cues are no longer informative (Reed et al., 2010). Further, in seabirds nestling growth is routinely used as an indicator of environmental conditions (Cairns, 1988). Inferences from such traits require an intimate understanding of the relationship between environmental variation and the measured biological trait (Grémillet and Charmantier, 2010; Brisson-Curadeau et al., 2017).

Nestling Growth and Demography

Weather effects on nestling traits can also affect the demographics of bird populations (Bryant, 1978; Salaberria et al., 2014). In many avian species, growth is likely to affect survival to fledging (nestling survival) and post-fledging survival (juvenile survival). In a review of predictors of juvenile survival, Maness and Anderson (2013) found (in a subset of quality-controlled studies) that nine out of ten studies identify an effect of nestling mass on juvenile survival, but noted that few studies assess whether growth rates affected juvenile survival. Given evidence that growth traits can influence nestling and juvenile survival (Maness and Anderson, 2013), the effects of variation in growth caused by weather patterns might most strongly affect demography in short-lived bird species (Sæther and Bakke, 2000). However, if nestling growth traits determine adult survival or fecundity, weather-induced nestling variation might change the demography of a broad range of avian species. During early life, environmental conditions, like weather, are expected to play a role in shaping adult phenotypes and fitness (Lindström, 1999). A meta-analysis of the effects of early developmental conditions in birds and mammals

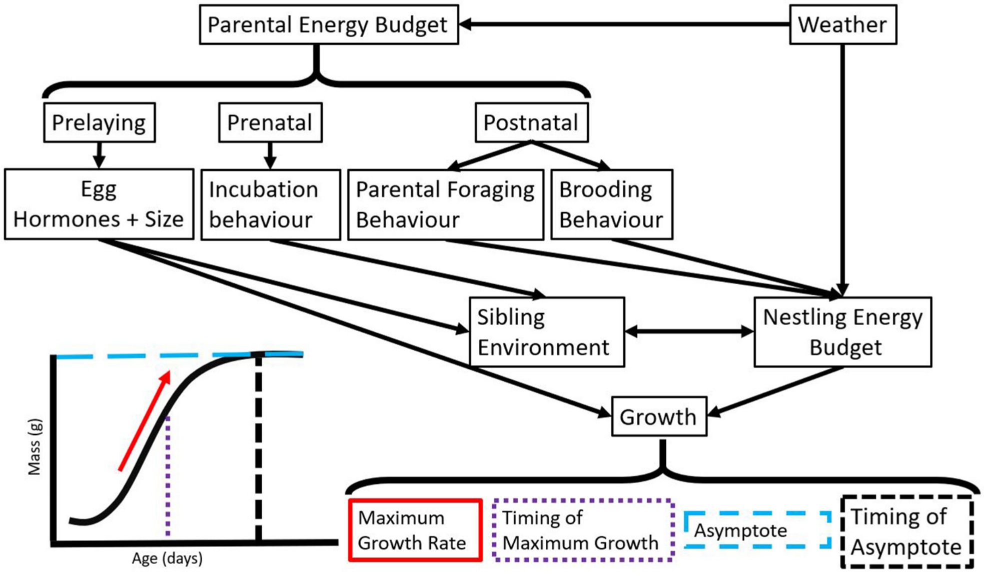

FIGURE 3 | Paths by which weather can impact variation in growth as described by parameters estimated from a general logistic curve. While we display physical growth in this figure, it will be useful to map the development of tissue functions (e.g., cognition, thermoregulation, motor function) onto this growth curve to compare and contrast development and physical growth over the nestling period. Many of the factors that impact growth are also likely to impact development.

found that poor early developmental conditions increases the rate of decline in fecundity with age, but developmental conditions do not influence the age-specific decline in survival in adults (Cooper and Kruuk, 2018). However, the latter result relies heavily on mammal studies, since only one avian study in this meta-analysis investigates the effects of the developmental environment on survival senescence (Hammers et al., 2013). Future studies on birds should investigate the effects of early life conditions (including weather) on traits expressed in adults.

DOCUMENTED WEATHER EFFECTS ON AVIAN GROWTH

Understanding current responses to weather enable us to extrapolate responses to predict future changes. Here, we review the effects of weather on growth and discuss the different ontogenic pathways through which weather could impact growth (**Figure 3**). To cover studies investigating the effect of weather on nestling growth, we searched in the ISI Web of Science on November 2nd, 2020. We used the keywords 'avian' OR 'bird' + 'growth' OR 'development' + 'climate change' OR 'global warming' OR 'weather' OR 'temperature' OR 'wind' OR 'rainfall' OR 'precipitation' OR 'sunshine' OR 'solar radiation' OR 'solar' OR 'insolation' OR 'experiment' + ' offspring' OR 'juvenile' OR 'nestling,' which brought up 989 references. We restricted papers to experimental and observational studies that examined the effect of weather variation on nestling growth, leaving 36 studies. Specifically, we retained studies that examined the effect of weather variables (wind, precipitation, solar radiation, temperature, ice- cover, sea-surface temperature) on nestling phenotypes during the growth period. Weather effects identified from our literature search are included in **Tables 1–4**.

Weather Impact of Growth Through Prenatal Effects

In addition to any effects of weather conditions on nestling growth in birds, conditions during embryonic development could affect post-hatching growth. A mother may influence the size of an egg and the hormones in an egg, potentially in response to environmental cues (Love and Williams, 2008; Bentz et al., 2013). The importance of egg size on nestling growth traits is somewhat uncertain. Effects of short-term weather variation on egg size tend to be limited (Nager and Noordwijk, 1992; Christians, 2002; Thomson and Hadfield, 2017; Griffith et al., 2020), and some studies note that egg size affects hatching traits, but this effect deteriorates through ontogeny (Krist, 2011; Williams, 2012).

Weather variation can, but does not always, influence maternal hormones transported into the egg, and these components can affect nestling growth (Schwabl, 1996; Groothuis et al., 2005; Addison et al., 2008; Groothuis and Schwabl, 2008; Ruuskanen et al., 2016). In particular, weather impacts on food may have a strong effect on maternal hormones deposited in the egg and could aid the matching of brood size to environmental conditions (Verboven et al., 2003; Gasparini et al., 2007; Vergauwen et al., 2012; Benowitz-Fredericks et al., 2013; Müller and Groothuis, 2013; Merkling et al., 2016). Other than hormonal influences, weather could also indirectly impact nestling growth through antioxidants, immunoglobins and antimicrobial agents (Williams, 2012), but these effects might be more indirect, as these compounds are less likely to affect growth directly and instead likely help nestlings survive in the face of environmental challenges (e.g., parasites).

If weather patterns during the prenatal period can predict the environment that a nestling will develop and grow in, a mother may be able to provide cues or influence the phenotype of her offspring to better match its future environment. However, the extent to which mothers provide such signals, and whether these signals are adaptive, is mostly untested in the wild. Whether a species has such cues may depend on the predictability of the environment it evolved in, and whether such cues remain adaptive will depend on how the predictability of the environment changes. Parents may even provide auditory cues to their prenatal offspring to signal warm environments resulting, for instance, in lighter 13-day old nestlings in zebra finches *Taeniopygia guttata* (Mariette and Buchanan, 2016).

Predicting changes in growth caused by climate change may depend on knowing the effects of an embryo's thermal environment on the nestling phenotype. Weather can directly affect the thermal environment that avian embryos experience and influence parental incubation behavior (DuRant et al., 2010; Griffith et al., 2016). Embryo thermal tolerance varies among species, with species from colder climates tending to have broader tolerances and lower optimums (Webb, 1987). However, even temperature variation within the range tolerated by an embryo can impact a nestling phenotype (Hepp et al., 2006; DuRant et al., 2010; Nord and Nilsson, 2011).

More experiments warming nest microclimates during incubation on a wide range of species might help clarify the impacts of a warmer incubation environment on nestling growth. Nest microclimate experiments are valuable because they reveal the combined effect of indirect thermal effects on the parents and direct effects on embryos (**Table 4**). Current results from experiments that warm the nest microclimate are variable and different species from the same study location can have contrasting effects on nestling growth (e.g., Mueller et al., 2019; **Table 4**). Few studies have experimentally cooled nests, but those that do find that it decreases nestling size and growth (**Table 4**). A cross-fostering experiment in tree swallows provides an interesting insight because nest warming during incubation increases the early age mass of nestlings incubated in a warm nest (raised by parents in a control nest) and the late-age mass of nestlings incubated in a control nest but raised by parents from a warm nest (Pérez et al., 2008). The cross-fostering experiment suggests carry-over effects of warming on parental care during growth and direct benefits of warming on young nestlings.

Post-hatching Weather Effects on Avian Growth

Variation in weather during the growth period is likely to affect chicks both directly and indirectly. Growth can be influenced

TABLE 1 | Associations between aspects of temperature and nestling growth traits identified from our literature search.

Species	Temperature variable	Association with growth	Study
Zebra Finch *Taeniopygia guttata*	Mean daily maximum during growth	Mean mass (–) and tarsus length (0)	Andrew et al., 2017
European bee-eater *Merops apiaster*	Mean daily maximum between hatching and measurements	Residual mass (0)	Arbeiter et al., 2016
Lesser kestrel *Falco naumanni*	Maximum during 2-day period before measurement	Mass gain in adobe cavity nests (–) Mass gain in wooden nest boxes (–)	Catry et al., 2015
European roller *Coracias garrulus*	Maximum during 2-day period before measurement	Mass gain in adobe cavity nests (0) Mass gain in wooden nest boxes (–)	Catry et al., 2015
Common fiscal *Lanius collaris*	Daily maximum	Diurnal change in mass at age 6 days (–)	Cunningham et al., 2013
Cliff Swallow *Petrochelidon pyrrhonota*	Mean daily maximum during growth	Nestling mass at age 10 days (–)	Imlay et al., 2018
Lance-tailed manakin *Chiroxiphia lanceolata*	Mean daily maximum during breeding season	Linear growth rate (–)	Jones and DuVal, 2019
Superb Fairy wren *Malurus cyaneus*	Mean maximum before growth	Mass at age 14 days (+, – quadratic)	Kruuk et al., 2015
Superb Fairy wren *Malurus cyaneus*	Mean maximum during period the end of the previous breeding season	Mass at age 14 days (–)	Kruuk et al., 2015
Lapland longspur *Calcarius lapponicus*	Mean maximum during growth	Daily growth rate (+)	Pérez et al., 2016
Pied flycatcher *Ficedula hypoleuca*	Mean and maximum between mass measurements	Age-specific mass at age 7, 10, and 13 days (+)	Siikamäki, 1996
Great tit *Parus major*	Mean daily during growth	Residual wing length (+)	Eeva et al., 2020
Pied flycatcher *Ficedula hypoleuca*	Mean daily during growth	Residual wing length (+, – quadratic)	Eeva et al., 2020
Pied flycatcher *Ficedula hypoleuca*	Mean during growth	Subarctic population residual mass (+) Temperate population residual mass (+)	Eeva et al., 2002
Wryneck *Jynx torquilla*	Mean hourly during the daytime between measurements	Daily growth of mass and 8th primary from age 14 to 16 days (–)	Geiser et al., 2008
White stork *Ciconia ciconia*	Mean daily during 7 days of growth	Relative growth rate (+)	Kosicki and Indykiewicz, 2011
Adelaide Rosella *Platycercus elegans adelaidae*	Mean day and night during growth Night-time standard deviation	Nestling linear growth in mass and bill surface area (+) Nestling linear growth in mass (–)	Larson et al., 2018
Blue tit *Cyanistes caeruleus*	Mean during 2-day period before measurement	Average 2-day increase in mass (–), head-bill length (–), tarsus length (–), fourth primary length (–)	Mainwaring and Hartley, 2016
Spotless starling *Sturnus unicolor*	Mean during growth of nestling from first brood Mean during growth of nestling from second brood	Wing length (+) and bill length (+) at age 14 days Mass (–), tarsus length (–), wing length (–), and bill length (–) at age 14 days	Salaberria et al., 2014
Curlew sandpiper *Calidris ferruginea**	Mean between growth measurements	Observed/expected growth of mass (+) Observed/expected growth of bill length (+)	Schekkerman et al., 1998
Chaffinch *Fingilla coelebs*	Mean daily minimum during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al., 2003
Linnet *Carduelis cannabina*	Mean daily minimum during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al., 2003
Skylark *Alauda arvensis*	Mean daily minimum during linear growth	Linear mass (+, – quadratic) and tarsus (+, – quadratic) growth rate	Bradbury et al., 2003
Yellowhammer *Emberiza citrinella*	Mean daily minimum during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al., 2003
Tengmalm's owl *Aegolius fenereus*	Mean daily during the breeding season	Nestling duration (0)	Kouba et al., 2015
Golden plover* *Pluvialis apricaria*	Mean daily minimum 2 days prior to measurement Mean daily minimum over age interval	Residual mass (0) Residual change in mass (+)	Machín et al., 2018

Temperature variables are sorted in the order maximum, mean, and minimum temperature and alphabetically by first author. Columns indicate the species, the weather variable found to be associated with a growth trait, the growth trait and whether the association was positive (+), negative (–) or not significant (0), and the study reference.
**Precocial species.*

TABLE 2 | Associations between aspects of precipitation and nestling growth traits identified from our literature search.

Species	Precipitation variable	Association with growth	Study
Canada goose *Branta canadensis*	Cumulative before and after hatch (June/July)	Principle Component 1 of Gosling Size (+)	Brook et al., 2015
Grasshopper Buzzard *Butastur rufipennis*	Cumulative post-hatch (June/July)	Days to grow from 10 to 90% of final mass (–) Grams per day mass gain from 0 to 10 days (+)	Buij et al., 2013
Tree Swallow *Tachycineta bicolor*	Cumulative 3 days prior to measurement	Residual mass (–)	Cox et al., 2019
Eurasian bittern *Botaurus stellaris*	Cumulative between measurements	Daily increase in mass (–) and tarsus length (–)	Kaspryzkowski et al., 2014
Pied flycatcher *Ficedula hypoleuca*	Cumulative between mass measurements	Age-specific masses at age 7, 10, and 13 days (–)	Siikamäki, 1996
European bee-eater *Merops apiaster*	Mean daily between hatching and measurement	Residual mass (0)	Arbeiter et al., 2016
Chaffinch *Fingilla coelebs*	Mean daily during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al., 2003
Linnet *Carduelis cannabina*	Mean daily during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al., 2003
Skylark *Alauda arvensis*	Mean daily during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al., 2003
Yellowhammer *Emberiza citrinella*	Mean daily during linear growth	Linear mass (–) and tarsus growth rate (–)	Bradbury et al., 2003
Wryneck *Jynx torquilla*	Mean hourly during the day between measurements	Daily growth of mass from age 3–5 and 5–7 days (–)	Geiser et al., 2008
Blue tit *Cyanistes caeruleus*	Mean daily 5 days prior to measurement	Nestling mass at age 11 days (+)	Grzędzicka, 2019
White stork *Ciconia ciconia*	Mean daily during 7 days of growth	Relative growth rate (–)	Kosicki and Indykiewicz, 2011
Tengmalm's owl *Aegolius fenereus*	Mean daily during the breeding season	Nestling duration (0)	Kouba et al., 2015
Fairy wren *Malurus cyaneus*	Mean before nestling growth	Mass at age 14 days (+)	Kruuk et al., 2015
Blue tit *Cyanistes caeruleus*	Mean during 2-day period before measurement	Average 2 days increase in mass (+), head-bill length (0), tarsus length (+), and fourth primary length (+)	Mainwaring and Hartley, 2016
Lapland longspur *Calcarius lapponicus*	Mean daily during growth	Daily growth rate (–)	Pérez et al., 2016
Gambel's white crowned sparrow *Zonotrichia leucophrys gambelii*	Mean daily during growth	Daily growth rate (–)	Pérez et al., 2016
Pied flycatcher *Ficedula hypoleuca*	Mean daily during growth	Subarctic population residual mass (0) Temperate population residual mass (0)	Eeva et al., 2002
Great tit *Parus major*	Maximum number of consecutive rainy days during growth	Residual wing length (+)	Eeva et al., 2020
Pied flycatcher *Ficedula hypoleuca*	Maximum number of consecutive rainy days during growth	Residual wing length (+)	Eeva et al., 2020

Precipitation variables are sorted in the order of cumulative, mean, and number of days with, precipitation and alphabetically by first author. Columns indicate the species, the weather variable found to be associated with a growth trait, the growth trait and whether the association was positive (+), or negative (–) or not significant (0), and the study reference.

by changes in thermal environments (e.g., Cunningham et al., 2013; McKinnon et al., 2013; **Tables 1**, **4**), and changes in food availability and parental care (e.g., Keller and Noordwijk, 1994). Scientists have long been interested in the effects of weather on growth and both historical and recent studies provide a baseline for making qualitative and quantitative predictions for changes in growth under different weather conditions (Lack and Lack, 1951; Hawksley, 1957; **Tables 1–4**). Predicting how climate change will impact avian growth depends on understanding how nestlings are affected by different weather components and how these weather components are expected to change under climate change.

A Warmer Growing Environment Can Positively or Negatively Impact Nestling Growth

Average global temperatures are expected to continue to increase with climate change, and for many regions, the frequency of heatwaves and variability of thermal environments are expected to increase (Intergovernmental Panel on Climate Change, 2018).

TABLE 3 | Associations between combined weather effects, wind speed, sunshine, and nestling growth traits identified from our literature search.

Species	Weather Variable	Association with growth	Study
Blue tit *Cyanistes caeruleus*	Mean wind speed during 2-day period before measurement	Average 2 day increase in mass (0), head-bill length (0), tarsus length (–), and fourth primary length (+)	Mainwaring and Hartley, 2016
Eurasian bittern *Botaurus stellaris*	Mean wind speed between measurements	Daily increase in mass (–) and tarsus length (–)	Kaspryzkowski et al., 2014
Tengmalm's owl *Aegolius fenereus*	Mean daily wind speed during breeding season	Nestling duration (0)	Kouba et al., 2015
European bee-eater *Merops apiaster*	Mean daily windspeed between hatching and measurement	Residual mass (0)	Arbeiter et al., 2016
	Mean daily sunshine between hatching and measurement	Residual mass (+)	Arbeiter et al., 2016
Chaffinch *Fingilla coelebs*	Mean daily sunshine hours during linear	Linear mass (0) and tarsus (0) growth rate	Bradbury et al., 2003
Linnet *Carduelis cannabina*	Mean daily sunshine hours during linear	Linear mass (0) and tarsus (0) growth rate	Bradbury et al., 2003
Skylark *Alauda arvensis*	Mean daily sunshine hours during linear growth	Linear mass (0) and tarsus (–) growth rate	Bradbury et al., 2003
Yellowhammer *Emberiza citrinella*	Mean daily sunshine hours during linear	Linear mass (0) and tarsus growth rate (0)	Bradbury et al., 2003
Barn Swallow *Hirundo rustica*	Temperature on day of nestling measurement Mean temperature between hatching and measurement	Nestling mass at age 8–12 days (–) – High wind speed dampened effect – High rainfall increased effect Nestling mass at age 8–12 days (–) – High wind speed dampened effect	Facey et al., 2020
American kestrel *Falco sparverius*	Principle Component 1 of weather during nestling growth period (associated with increased wind, rainfall, and cold air temperature)	Nestling mass (–) and length of tenth primary (–) at age 20.5–24 days	Dawson and Bortolotti, 2000

Columns indicate the species, the weather variable found to be associated with a growth trait, the growth trait and whether the association was positive (+), negative (–), or not significant (0), and the study reference.

Increasing temperatures can result in either challenging or improved growing conditions for nestlings and can operate either directly through thermal changes experienced by nestlings or indirectly by affecting parents' foraging or brooding behavior (Andreasson et al., 2020b; **Table 1** and **Figure 3**). The effects of warming may vary among species, populations, and environments because some populations may be closer to their thermal limits or may be more susceptible to dehydration. For example, species living in environments below their thermal optimum may benefit from increased natural air temperatures during development (e.g., McKinnon et al., 2013), while increased air temperatures or heatwaves may have strong negative impacts on species living close to their thermal limits (Conradie et al., 2019). The effect of thermal changes depends on the ability of nestlings to thermoregulate. If temperatures are beyond a nestling's thermal neutral zone (the temperature range that body temperature is maintained with little energy expenditure), nestlings will have inefficient physiological processes unless they allocate energy to thermoregulation. Further, nestlings might use limited energy resources on thermoregulation, instead of growth, to prevent body temperatures outside their thermal maximum (e.g., Andreasson et al., 2018).

In many bird species, warmer temperatures are associated with faster growth, heavier asymptotes, heavier age-specific masses, or have no effects at all (Dyrcz, 1974; Hiraldo et al., 1990; McCarty and Winkler, 1999; see **Table 1**). But, warming temperatures can also correlate with slower growth and smaller nestlings. In a population of blue tits in Lancashire in the United Kingdom, warmer air temperatures correlate with slower increases of tarsus length, head size, feather length, and body mass (Mainwaring and Hartley, 2016), and in nestling Eastern kingbirds *Tyrannus tyrannus* high temperatures covary with smaller age-specific masses (Murphy, 1985). Similarly, in arid environments, warmer temperatures correlate with smaller nestlings (Cunningham et al., 2013; Wiley and Ridley, 2016; Andrew et al., 2017; Van de Ven, 2017). In arid environments, warming may frequently approach the thermal maximum of many bird species, resulting in smaller nestlings and increases in nestling mortality either from decreases in parental foraging or direct challenges for nestlings (Cunningham et al., 2013; Wiley and Ridley, 2016; Van de Ven, 2017; Conradie et al., 2019). Studies that experimentally heat passerine nestlings tend to find that warmer conditions slow growth and result in smaller nestlings in warm climates (Rodríguez and Barba, 2016b; Andrew et al., 2017; **Table 4**), but that warmer conditions have a positive or mixed effect on nestling mass and size in cool temperate environments (Dawson et al., 2005; Andreasson et al., 2018; **Table 4**). In many instances, it will be important to explore specific aspects of temperature (e.g., maximum, minimum, mean) because they may affect growth differently (**Table 1**). For

TABLE 4 | Associations between experimental manipulations of environmental conditions and nestling growth traits.

Species	Experimental manipulation	Association with growth	Study
Blue Tit *Cyanistes caeruleus*	Heating of nest during growth	Increase in mass with age (–) Tarsus and wing length at age 14 days (0)	Andreasson et al., 2018
Zebra Finch *Taeniopygia guttata*		Mass and tarsus length at age 28 days (–)	Andrew et al., 2017
Tree Swallow *Tachycineta bicolor*		Growth rate constant of mass (+), length of ninth primary feather (+), and length of tarsus (0)	Dawson et al., 2005
Great Tit *Parus Major*		Mass at age 15 days (–)	Rodríguez and Barba, 2016b
Great Tit *Parus Major*	Cooling of nest during growth	Mass at age 15 days (0) Tarsus length at age 15 days (–)	Rodríguez and Barba, 2016a
Great Tit *Parus Major*	Heating of nest during incubation	Age-specific tarsus length, and mass (0) Mass and tarsus length growth rate (0)	Álvarez and Barba, 2014
Carolina Wrens *Thryothorus ludovicianus*		Nestling period (–) Mass at age 9 days (–)	Mueller et al., 2019
European starlings	Heating of nest during incubation	Nestling period (0) Mass at age 3 days (0) Ratio of mass to tarsus cubed at age 10 days (0)	Reid et al., 2000
Prothonotary warbler *Protonotaria citrea*		Nestling period (–) Mass at age 8 days (+)	Mueller et al., 2019
Tree Swallows *Tachycineta bicolor*		Variation in mass at 1 day of age (–)	Ardia et al., 2009
	Heating at origin nest during incubation Heating at nest of rearing during incubation	Residual Mass at age 4 and 7 days (+) Residual Mass at age 10 and 13 days (+)	Pérez et al., 2008
	Cooling at origin nest during incubation	Residual (–) and absolute mass (–) at age 4 and 7 days	Ardia et al., 2010
	Cooling at nest of rearing during incubation		
	Cooling nest temperatures during incubation	Absolute mass at age 10 days (–)	
Blue tits *Cyanistes caeruleus*		Growth rate (–) Mass at age 14 days (–)	Nilsson et al., 2008
Mountain blackeye *Chlorocharis emiliae*	Warming of nest and rain protection during incubation and growth	Nestling period (–), mass growth rate constant (+), wing length growth rate constant (+), tarsus length growth rate constant (+)	Mitchell et al., 2020
Tree Swallow *Tachycineta bicolor*	Experimental trimming of female ventral feathers	Nestling asymptotic mass (+)	Tapper et al., 2020
Blue tits *Cyanistes caeruleus*	Experimental trimming of parent's ventral feathers (Control and experimental broods were both enlarged)	Mass of nestlings at age 14 days (+) – Only for first time breeding females Wing length (+) and tarsus length (0) at age 14 days	Nord and Nilsson, 2019
	Experimental trimming of parent's ventral feathers (Control and experimental broods were both enlarged)	Mass (0), tarsus length (0), and wing length (0) at age 14 days	Andreasson et al., 2020a

Columns indicate the species, the weather variable found to be associated with a growth trait, the growth trait and whether the association was positive (+), negative (–), or not significant (0), and the study reference.

example, crimson rosella *Platycercus elegans* nestlings are heavier when the minimum nest temperature is high, but nestlings are lighter when the mean nest temperature is high (Larson et al., 2015). Finally, birds that produce several broods could face different weather conditions for each brood. For example, because temperatures are warmer when spotless starlings *Sturnus unicolor* produce their second brood, increasing temperatures result in smaller 14-day old nestlings, while the opposite effect is found for first broods (Salaberria et al., 2014). Different temperature regimes during early and late broods suggest nestlings in late broods might be more strongly impacted by warming conditions unless parents can adjust nesting locations (presumably to cooler locations) for their second broods.

Sensitivity to Thermal Variation Could Vary Throughout Nestling Ontogeny

To understand the impacts of temperature variation, we also need to investigate the potentially varying impacts of a thermal challenge during different time points in ontogeny. To predict warming effects on growth patterns it may be important to identify periods of weather within a season that might impact growth and determine how these time periods are predicted to change.

Development of thermoregulation varies among species, but endothermy develops after hatching in birds and earlier during ontogeny in precocial species than in altricial species (Dunn, 1975; Whittow and Tazawa, 1991; Nichelmann and Tzschentke, 2002; Price and Dzialowski, 2018). Because of better thermoregulatory abilities, young precocial nestlings may be better able to survive temperature challenges than young altricial species (Hohtola and Visser, 1998). Within a species, mass is an important determinant of thermoregulatory ability (Visser, 1998), but most studies investigate relationships between size and thermoregulation among species and it is unknown how this relates to variation among nestlings within a species. In the context of a warming environment, smaller birds could be better able to cope with heat stress through faster evaporative cooling (McKechnie and Wolf, 2010), but evaporative cooling causes water loss, leaving small birds vulnerable to dehydration (Whitfield et al., 2015). Consequently, small nestlings may be more susceptible to high temperatures in water-limited environments than large nestlings because of potential dehydration (Whitfield et al., 2015). However, many small birds that live in hot and arid environments will have adaptive strategies, like facultative hyperthermia, that allow tolerance of challenging high temperatures (Gerson et al., 2019; Freeman et al., 2020).

To predict the effects of a warming environment on avian growth, it will be important to know whether hot temperatures during early life can improve tolerance of warmer environments later in life. Evidence from poultry suggests temperature conditioning during incubation and early ages can improve growth performance in warm and cold environments (Nichelmann and Tzschentke, 2002; Shinder et al., 2002; Loyau et al., 2015; Oke et al., 2020; reviewed in Nord and Giroud, 2020). No study has investigated the effects of short-term prenatal exposure to hot or cold temperatures in wild birds, but continuous exposure to low incubation temperatures generally reduces a nestling's thermal regulatory ability (reviewed in Nord and Giroud, 2020).

How Does Adult Thermoregulation Relate to Offspring Thermoregulation?

According to the 'climate variability hypothesis,' high latitude birds may be better able to tolerate temperature variation (Stevens, 1989). This hypothesis suggests that organisms that experience more variable climates should have wider thermal tolerances, and climate variation tends to increase with latitude (Stevens, 1989). A meta-analysis of non-migratory birds supports the climate variability hypothesis – adults of bird species living in variable environments can tolerate a broader range of temperatures (Khaliq et al., 2014). Importantly, migratory bird species do not demonstrate a trend toward increased or decreased tolerance to environmental conditions with latitude. However, when trying to predict the impacts of weather changes on bird species, the variability of the environments where the species evolved may be important. Given this empirical result on adults, we might predict that the offspring of species adapted to more variable environments can tolerate more warming. Note, however, that the relevance of tolerance in adults depends on how tolerance of offspring is related to adult tolerance. If offspring have broader or narrower thermal niches than adults, they may have better or worse resilient than adults to direct effects of temperature challenges. No studies of wild birds have measured thermal tolerance development and compared it to adult birds' thermal tolerance (Nord and Giroud, 2020).

Weather Impacts Growth Through Changes in Food Availability

Weather variation affects the timing of food abundance, which, depending on when reproduction occurs, can affect the food available for nestling growth (Naef-Daenzer and Keller, 1999; Both et al., 2006; Daunt et al., 2006; Visser et al., 2006). Major components of climate change are shifts in the mean and variability of weather conditions. A consequence of shifting weather conditions is that cues used by birds to time their breeding may become unreliable predictors of food abundance (Bonamour et al., 2019). The mismatch hypothesis suggests that species at lower trophic levels are better able to track shifts in climatic variation than are those at upper trophic levels, resulting in top consumers being less able to time their reproductive events to match food abundance (Stenseth et al., 2002; Thackeray et al., 2016). Because of changing or variable climatic conditions, many birds may have fewer available food resources while offspring develop. For example, both rainfall changes and an inability to temporarily track shifts in prey species can decrease food availability during nestling growth (e.g., black kites *Milvus migrans* Hiraldo et al., 1990; Lapland longspurs and white crowned sparrows Pérez et al., 2016). In Baird's sandpiper *Calidris bairdii*, increases in asynchrony of hatching date with peak biomass of crane flies (Tipulidae) correlates with a slower maximum growth rate (McKinnon et al., 2012). In thick-billed murres *Uria lomvia*, earlier ice break-up covaries with decreases in Arctic cod *Boreogadus saida* and increases in capelin *Mallotus villosus* in the murre diet. Further, hatching later relative to the ice breakup is associated with smaller 14-day old nestlings (Gaston and Elliott, 2014).

Some avian nestlings demonstrate a remarkable ability to persist under periods of scarce food. Laboratory research and avian husbandry suggest that, in some bird species, nestling growth is incredibly flexible in response to food restriction. Chickens *Gallus gallus domesticus*, Japanese quail *Coturnix japonica*, and mallards *Anas platyrhynchos* raised on restricted diets pause their growth (sometimes for months) then resume typical growth trajectories when food restriction stops, with no evident effect on adult morphology (Jordan, 1953; Singsen et al., 1964; reviewed in Schew and Ricklefs, 1998). Similarly, some seabird species can slow chick growth and delay fledging in years with low food abundance or poor weather conditions (Barrett and Rikardsen, 1992; Weimerskirch et al., 2001; Chiaradia and Nisbet, 2006; Kuepper et al., 2018), and white-fronted bee-eaters *Merops bullockoides* can pause growth during periods of low food availability (Emlen et al., 1991). Some species can maintain growth early in the nestling stage because of spare yolk

(Romanoff, 1944), but nestlings may be more vulnerable to food shortages when the yolk is depleted. For many species extending growth will not be possible because the time window for breeding is restricted (e.g., many Arctic breeding birds). If the timing of the breeding season is constrained, it may be optimal to mature at a smaller size rather than arrest growth until suitable food sources become available.

Life-History Strategy May Determine How Parental Care Changes Under More Difficult Weather Conditions

Weather can also have indirect effects on growth by influencing the foraging or brooding behavior of parents (Taylor, 1983; Machmer and Ydenberg, 1990). The degree to which birds can adjust their parental effort is likely to depend on their life-history, possibly resulting in differing magnitudes of impacts of weather variation in species with high versus low adult survival (Ghalambor and Martin, 2001). For instance, under unpredictable or stressful conditions, long-lived species may invest less in reproductive effort, including parental care, with a stronger impact on nestling growth. All species face trade-offs in their allocation of resources into reproduction and survival (Stearns, 1989). These trade-offs may be particularly apparent in altricial species and in species with nestlings dependent on parents for food or thermoregulation. Parents can cope with fewer resources by increasing foraging effort at the expense of their body condition – helping chicks to survive challenging weather conditions. For example, in tree swallows, increases in rainfall correlate with increases in parental provisioning at the expense of declines in adult body condition (Cox et al., 2019). Alternatively, parents may invest less in reproduction during stressful situations to preserve or maintain their body condition. Yellow-nosed albatrosses *Diomedea chlororhynchos* appear to increase provisioning in response to poor nestling condition only if food is plentiful, limiting the costs of reproduction for themselves in unfavorable years (Weimerskirch et al., 2001). Future work could determine which strategy is adaptive for different life-histories under unpredictable or extreme food conditions.

Other Components of Weather Can Also Affect Nestling Growth

Climate change is increasing the frequency of heavy precipitation events (Intergovernmental Panel on Climate Change, 2018), and rainfall can have variable effects on avian growth (**Table 2**). The effects of rainfall on nestling growth may depend on when rainfall occurs relative to a species' breeding season (Kruuk et al., 2015). During nestling growth, rainfall can decrease growth rates and age-specific morphometrics (Siikamäki, 1996; Kosicki and Indykiewicz, 2011; Kaspryzkowski et al., 2014; Pérez et al., 2016; Cox et al., 2019, but see Mainwaring and Hartley, 2016; Grzędzicka, 2019; **Table 2**). Decreases in growth can result from nestlings having difficulty thermoregulating because of wet downy feathers or difficult foraging conditions for parents (Nye, 1964; Keller and Noordwijk, 1994). In great tits, days with some rainfall greater than 1 mm result in decreases in daily mass gain by nestlings. The negative association between rainfall and daily mass gain in great tit nestlings is suspected to be caused by decreases in foraging of parents because experimental trapping of adults has negative effects on growth comparable to daily rainfall (Keller and Noordwijk, 1994). In hot and dry regions, prey abundance may increase in rainy conditions and will improve foraging conditions for parents and nestling growth rates (Sicurella et al., 2014).

In some studies rainfall has mixed effects on growth or only impacts nestlings at specific ages. Robinson et al. (2017) categorized 3 years of their study on Arctic peregrine falcons *Falco peregrinus tundrius* as cool and wet or as warm and dry. In cool and wet years, nestlings grew the fastest, grew to a lower-than-average asymptote, and attain their maximum growth rate at a younger age (Robinson et al., 2017). In little auks *Alle alle*, rainfall during the nestling period correlates with decreases in the masses of young nestlings, while in red-capped larks *Calandrella cinerea* monthly rainfall has a positive effect on the mass of older nestlings, but no effect on young nestlings (Konarzewski and Taylor, 1989; Ndithia et al., 2017).

In contrast to rainfall during nestling growth, rainfall outside the breeding season might increase avian growth rates and masses because of the generally beneficial effects of rainfall on vegetation and insect abundance. In a population of superb fairy wrens *Malurus cyaneus*, increases in rainfall prior to nestling growth result in heavier nestling masses (Kruuk et al., 2015). Higher rainfall during the nestling stage is associated with increases in gosling size in the Canada goose *Branta canadensis*, but the authors suggest that high rainfall during growth is likely associated with high rainfall prior to the nestling stage (Brook et al., 2015). The authors suggest that disentangling whether rainfall during growth had a negative effect on Canada goose nestling growth might be hard because the observed effect was a combination of earlier rainfall effects on vegetation and direct effects of rainfall on nestling size.

In many regions, global climate change is expected to increase ocean wind speeds but decrease land wind speeds (Torralba et al., 2017). Increases in wind speeds often correlate with lower age-specific nestling masses in seabirds. Common terns *Sterna hirundo*, for example, display reductions in growth when wind speeds are high (Langham, 1968), maybe because of a reduction in the ability of parents to capture prey (Taylor, 1983). Interestingly, high wind speeds do not appear to affect nestling growth of a relative of common terns, sandwich terns *Thalasseus sandvicensis*, perhaps because of differences between these two species in foraging behavior or morphology (Langham, 1968; Taylor, 1983). In the little auk, wind speed and decreases in visibility correlate with lower masses in nestlings older than 5 days (Konarzewski and Taylor, 1989). Environmental differences at breeding locations might determine whether a weather variable impacts growth in black-legged kittiwakes *Rissa tridactyla*, wind speeds do not affect nestlings on a colony in the Gulf of Alaska, but high wind speeds do reduce the growth of nestlings on a colony in the Norwegian Sea (Elliott et al., 2014; Christensen-Dalsgaard et al., 2018). Marine birds may need to change or increase their foraging behavior with changing weather conditions, or offspring will need to adjust to lower or variable food provisioning.

Components of foraging behavior in birds can vary among individuals, and individuals may change their behavior differently in response to weather conditions (Woo et al., 2008; Patrick et al., 2014). Differences among individuals in foraging and how foraging behavior develops may be essential to determine which strategies are adaptive in an altered environment. Beyond effects on foraging, wind may stress (e.g., via noise) nestlings directly, resulting in altered growth phenotypes (Crino et al., 2020). Evidence from blue tits suggests that increases in wind speeds negatively affect the growth of fourth primary feathers, mass and tarsus, so a decline in average wind speeds on land may result in more favorable growing conditions for some land birds (**Table 3**; but see Sicurella et al., 2014).

Variation in sea-surface temperature is also likely to impact food availability for many seabirds. Average sea-surface temperatures are expected to increase globally, with some regions warming more rapidly than others (Intergovernmental Panel on Climate Change, 2013). Sea-surface temperature changes are likely to affect marine bird species by changing their prey species' distribution, abundance, and phenology, generally resulting in lower food availability and, in extreme cases, in mass seabird die-offs (Piatt et al., 2020). Associations between warm sea-surface temperatures and slower daily mass gain are found in numerous seabird species (Bertram et al., 1991; Hedd et al., 2002; Gjerdrum et al., 2003; Smithers et al., 2003; Peck et al., 2004; Ancona et al., 2011; but see Pinaud et al., 2005). Additionally, sea-ice coverage, age, and distribution will be important for provisioning in ice-associated seabirds (Gaston and Elliott, 2014; Divoky et al., 2015). Generally, increases in sea-surface temperatures correlate with decreases in nestling masses in seabirds, likely because of low prey availability during breeding.

Lastly, the interaction of different weather effects may change our predictions of future change because interactions among weather variables or other changing variables could enhance or ameliorate negative effects. For example, in a study of barn swallows *Hirundo rustica*, nestling mass between age 8–12 days is negatively associated with increasing temperatures, and this effect is stronger during heavier rainfall, but weaker during high wind speeds (Facey et al., 2020).

Variation in Weather Conditions May More Strongly Impact Later-Hatching Nestlings

The hatching order of a nestling within a brood might play an important role in how weather interacts with growth. In species with asynchronous hatching, older nestlings can outcompete younger nestlings for food, and younger nestlings will frequently grow more slowly, fledge at a smaller size, or die from starvation or aggression from older nestlings (Mock and Parker, 1998). Siblicide can be facultative or obligate. When siblicide is facultative, aggression and siblicide within a brood may be less frequent when food availability and weather conditions are favorable (e.g., Bortolotti et al., 1991; Reynolds, 1996). Egg-hormones, parental incubation, and parental feeding behavior might all modulate competition among nestlings (Mock and Parker, 1997; Müller and Groothuis, 2013). Weather conditions could act as cues for changes in physiology or behavior that promote or impede competition among nestlings. If climate change generally results in weather conditions that are unfavorable for growth (less food, increased thermal stress), the strongest impacts of changing weather conditions will likely be on later hatching nestlings.

WEATHER AND THE EVOLUTION OF AVIAN GROWTH

Because weather can influence avian growth in many ways, a change in weather will likely result in altered selection on nestling growth traits and influence the evolution of nestling growth traits that are heritable. To predict the evolution of avian growth traits, we need to understand the evolvability of these traits as well as natural selection acting on them. Both these components of evolution, i.e., growth evolvability and natural selection on growth, can change according to environmental variations.

Estimation of the Evolutionary Potential of Growth Is Challenging

Little is known about the heritability of nestling growth traits under different weather conditions, making it difficult to predict how and whether nestling traits will evolve in response to changing climate. Similarly, little is known about how variation in weather affects natural selection on growth traits.

Fewer studies have investigated the heritability of growth parameters such as the asymptote, growth rate, and timing of maximum growth (**Figure 1**) in the wild. Tarsus length at 13–15 days of age in European starlings is heritable when analyzed using either offspring-midparent regressions (h^2 = 0.43 [*SE* = 0.12]) or full-sibling analyses (h^2 = 0.30 [*SE* = 0.22]) in a partial cross fostering experiment (Smith and Wettermark, 1995). Such high heritability for tarsus length is similar to findings of many other avian quantitative genetic studies (Postma and Brommer, 2014). However, when Smith and Wettermark (1995) used an analysis of variance to estimate the heritability of logistic growth curve components fit to the starling's masses, they found the asymptote to be heritable (h^2 = 0.25 [*SE* = 0.21]) but not the inflection point or growth constant. Age-specific size and mass measurements also have been found to be heritable in medium ground finches, and great tits (h^2 of fledging mass = 0.24 [*SE* = 0.02]; Garant et al., 2005).

Advances in statistical techniques used in quantitative genetics now allow a more accurate measurement of the evolutionary parameters of nestling growth in wild populations. Mixed models called 'animal models' that use between-individual relatedness within a population and can handle uneven sampling designs offer an improvement over offspring-midparent regressions (Kruuk, 2004; Wilson et al., 2010). Use of an animal model in house sparrows shows the nestling age-specific masses and tarsus lengths to be heritable (h^2 for mass at 5 days = 0.57 [*SE* = 0.19], mass at 10 days = 0.86 [*SE* = 0.13]; tarsus at 5 days = 0.81 [*SE* = 0.22], tarsus at 10 days = 0.63 [SE = 0.11]; Bonneaud et al., 2009). In a more recent large cross-fostering experiment of blue tits, age-specific masses throughout a nestling's growth period are found to have low heritabilities using an animal model (h^2 ranged from 0.07 [*SE* = 0.04] at 0 days to 0.09 (*SE* = 0.03] at 6 days (Hadfield et al., 2013). The authors attributed the low additive genetic variances and heritabilities of nestling age-specific masses to their multivariate statistics and experimental design, where they controlled for the effects of viability selection when estimating (co)variances among nestlings (Hadfield et al., 2013). Analyses accounting for missing data from individuals that do not survive until nestling mass measurement can help avoid biases in estimates of selection and additive genetic variances for nestling traits (see Hadfield, 2008 for a thorough discussion)

In poultry, the heritability of growth parameters (asymptote, the timing of maximum growth, growth rate, age-specific mass/size) can be moderately heritable (e.g., h^2 range = 0.15 – 0.66; Grossman and Bohren, 1985; Mignon-Grasteau, 1999; N'Dri et al., 2006; Dana et al., 2011; Haunshi et al., 2012) and selection on domestic species provides evidence that growth traits can evolve under these controlled settings (Marks, 1990 as cited in Steigner et al., 1992; Noordwijk and Marks, 1998; Zuidhof et al., 2014). Heritability of avian growth might be higher in husbandry settings compared to wild populations because of controlled rearing conditions, which reduce the amount of environmental variation. Quantitative genetic studies on avian growth in wild conditions are presently too scarce to make more robust conclusions on the expected levels of heritability, so we encourage more studies to estimate the additive genetic variance of nestling growth parameters in wild avian populations.

Heritability Is Environmentally Dependent

An important note relevant to weather conditions is that heritability measures are only applicable to the population and the environment where they are measured. The denominator in the calculation of heritability, phenotypic variance, is equal to the sum of genetic variance and environmental variance. Hence, an increase in the environmental variance of a trait results in a decrease in the heritability estimate. Additionally, environmental variation can impact the level of additive genetic variation estimated for a given trait (Gebhardt-Henrich and Noordwijk, 1994; Charmantier and Garant, 2005; Wood and Brodie, 2016). Early papers measuring the heritability of growth traits noted that poor environmental conditions during growth might restrict the expression of additive genetic variance, resulting in lower heritability of the fledgling or adult phenotypic traits in unfavorable environments (Gebhardt-Henrich and Noordwijk, 1991, 1994; Gebhardt-Henrich, 1992). The original hypothesis of environmental influence on the heritability of growth by Noordwijk (1982 as cited in Noordwijk and Marks, 1998) suggests that under unfavorable conditions, a nestling might not reach its genetically determined size, but instead would be constrained because of maturation at a set age. However, under favorable conditions a nestling will reach a final size before age-induced maturation. Therefore, the hypothesis suggests that variation in the asymptote under unfavorable conditions might be more likely to reflect environmental differences among nestlings and the variation under favorable conditions might reflect genetic differences among individuals (Noordwijk and Marks, 1998). A change in the genes that underlie the phenotypic expression of a trait could also cause a change in additive genetic variation between environments (Wood and Brodie, 2016). For example, in a hot environment, genes that play a role in heat tolerance might largely determine the additive genetic variance in a growth trait, while in a thermoneutral environment, genes that play a role in metabolism and growth might explain most of the differences among individual growth trajectories. Therefore, weather variation could affect rates of evolution through an increase or decrease in heritability by increasing or decreasing the environmental and/or the additive genetic contribution to variation in nestling growth traits. Lastly, because heritability is dependent on environmental variance, directly reporting the additive genetic variance of a trait scaled by the mean will allow accurate comparisons of evolvability across traits and species (Houle, 1992; Hansen et al., 2011). It is important for researchers to report both metrics when trying to evaluate the general evolvability of any trait.

While we might not know how heritability will change with different weather patterns, we do know that annual changes in the heritability of nestling size traits in response to changes in environmental conditions have been observed. Following a brood size manipulation experiment in great tits, Gebhardt-Henrich and Noordwijk (1991) found that heritability of mass at 15 days of age (near asymptotic mass) might be lower in large broods (average h^2 = 0.40 [SE = 0.54]) than in small broods (average h^2 = 0.75 [SE = 0.36]), but only in years when environmental conditions are unfavorable. Notably, standard errors are large, and results are not statistically significant, but this study is one of the earliest to postulate an effect of environmental conditions on evolutionary parameters in nestling traits. In a comparison of age-specific size measurements following a brood size manipulation in blue tits, Kunz and Ekman (2000) detected high heritability estimates for age-specific tarsus (age 8 and 10 days), wing (age 6 days), and mass (age 6 and 8 days) measurements in smaller compared to larger broods. While not focused on weather conditions, other more recent studies have noted higher heritability in more favorable environments (Charmantier et al., 2004; Garant et al., 2005).

Experimental studies on poultry provide insight into how weather impacts might influence the evolutionary response of chick growth traits. Marks (1996) examined the response to artificial selection for increased 4-week body mass in restricted versus full nutritional diet lines of Japanese quail (*Coturnix japonica*) and found that the restricted diet line had much lower phenotypic increases (no changes in phenotype for many generations) in 4-week body mass. The quail chick's growth conditions are artificial but could indicate that evolutionary changes in nestling size will be slower in environments where weather conditions reduce food availability, as is expected for climate change in many ecosystems.

Generally, these studies indicate that the heritability of fledging mass increases under favorable conditions, but we should cautiously extrapolate from the current literature because the taxonomic range of current results is restricted, and many studies do not investigate the effects of weather. Further, no studies to our knowledge evaluated the changing heritability of growth rates or the timing of maximum growth in wild populations.

Perspectives on Adding Complexity and Interactive Effects

Beyond the genetic variance of a trait, the evolution of a trait also depends on its genetic covariance with other traits (Willham, 1972; Arnold et al., 2008; Walsh and Lynch, 2018). The evolution of growth traits may be constrained because of genetic correlations among traits. For example, genes that increase asymptotic mass may decrease the maximum growth rate. Therefore, weather variation could affect the evolution of growth traits by influencing the genetic covariance among traits. To date, no study has investigated how weather variation shapes genetic covariances among chick growth traits. Hence it is difficult to determine if genetic constraints or the effect of weather on genetic constraints will have an important role in the evolutionary response of avian growth traits to climate change.

Finally, in addition to a given growth trait's evolutionary trajectory being dependent on genetic correlations, selection on growth traits induced by climate change can interact with other selective forces. For instance, comparative studies have shown that adult and nestling birds are repeatedly smaller in cities than in surrounding rural areas (Bailly et al., 2016; Caizergues et al., 2018). However, as with weather effects, such trends have not yet been attributed to either plastic or evolutionary processes. Several factors that directly influence growth and are affected by climate change (e.g., food availability) are also affected by growing urbanization. Predictive models will hence need at some point to include the complexity of these different and interacting selective forces. Some authors (e.g., Grimm et al., 2008) have hypothesized that since urban areas are 'heat islands,' cities provide an interesting opportunity to study how global warming will impact specific traits (Rivkin et al., 2019). Describing growth curves in urban birds could, hence, be informative in understanding how warmer temperatures and changes in resources influence avian growth. Gene flow from populations adapted to urban habitats into populations in more natural habitats could also provide individuals pre-adapted to warmer conditions (e.g., adaptation with gene flow; Tigano and Friesen, 2016).

CONCLUSION

Human-induced warming has resulted in average global temperatures increasing by 1°C since the preindustrial period, and temperatures are likely to increase by 1.5°C or more in the next 2–3 decades (Intergovernmental Panel on Climate Change, 2018). If the impacts of weather on a species are known, qualitative or quantitative predictions for growth trait changes from weather-growth models can be used to predict future growth trait changes. If the additive genetic variance and fitness associated with differences in growth traits can be estimated, these models could be improved with evolutionary and demographic information (Jenouvrier and Visser, 2011; Vedder et al., 2013).

We have outlined multiple weather components that affect growth traits of avian species. The future of this research will involve trying to predict adaptive responses to these changes. We think the main questions to address next are: (1) what growth trajectories are adaptive in an environment altered by climate change? (2) what is the potential for a given population of birds to adapt to climate change through either plastic or evolutionary adjustments in growth and development? (3) how will environmental changes alter parental effects on growth? and (4) is the potential for adaptation of growth or development altered by the predictability of weather or environmental conditions? To answer these questions, we need more information on the relationship between individual fitness and growth curves and the genetic (co)variance of chick growth traits.

AUTHOR CONTRIBUTIONS

DS conducted the literature review. DS, VLF, and AC conceived the project idea and wrote the manuscript. All the authors contributed to the article and approved the submitted version.

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