BEHAVIORAL ADAPTATIONS TO LIFE IN THE CITY

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BEHAVIORAL ADAPTATIONS TO LIFE IN THE CITY

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Table of Contents

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EDITORIAL
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Editorial: Behavioral Adaptations to Life in the City

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Editorial on the Research Topic

Behavioral Adaptations to Life in the City

Humans have drastically transformed the planet and recent estimates indicate that only 3% of terrestrial ecosystems remain ecologically intact (Plumptre et al., 2021). A fundamental challenge of ecologists, evolutionary biologists, and conservation practitioners is to understand how animals are responding to these rapid ecosystem changes and novel environments. Urban regions are among the newest and most rapidly expanding habitats as well as the most altered terrestrial ecosystems on the planet (Grimm et al., 2008; Seto et al., 2012; Rivkin et al., 2019). Studies that focus on urban phenotypes and seek to understand what traits permit animals to permeate the urban filter, have provided a greater understanding of which animals and functional groups are best able to adapt to novel urban environments. In addition, population-level studies that focus on changes in physiology, morphology, and behavior have elucidated the manners in which animals are most likely to adapt and survive in urban areas. However, it is not entirely clear what aspects of urban living are responsible for urban phenotypes or if urban adaptations lead to meaningful divergence from rural populations.

Urban environments present novel abiotic and biotic environments for species. Novel abiotic changes include anthropogenic noise, artificial light, heat islands, and chemical pollution, all of which strongly influence animal behavior, physiology, and population density (Swaddle et al., 2015; Sparkman et al., 2018; Putman et al., 2019). Novel biotic changes include shifted diets and foraging opportunities, depauperate faunal communities, heightened levels of non-native species and altered predator communities (Isaksson and Andersson, 2007; Narango et al., 2017; Seress et al., 2018). Understanding how animals respond and adapt to these novel environmental factors can help us understand which species are able to adapt to urban environments, and how urban environments might be altered to accommodate more native species.

This special issue on *Behavioral Adaptations to Life in the City* brings together a collection of articles to explore fundamental questions that to date have been unanswered. The goal of the special issue is to explore these questions, fill in knowledge gaps regarding urban phenotypes and present the latest theoretical and empirical research on behavioral flexibility and adaptations to urban environments. With the recent pandemic came increased awareness of animal life in cities, and these studies address the recent surge in interest as to how animals succeed or fail in urbanized habitats. The special issue identifies traits of the urban phenotype and discusses potential fitness consequences of those traits.

Several papers in this issue confirm and expand upon many specific traits, such as bird song and nesting behavior, that have been observed or hypothesized to be typical of the urban phenotype. For example *Variation in Diurnal Patterns of Singing Activity Between Urban and Rural Great Tits* by Bermúdez-Cuamatzin et al., find differences in singing activity of great tits between urban and rural areas such that urban tits sing earlier during the day,

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with similar singing effort during the dawn chorus and lower singing effort later during the day as compared to rural birds. *Temporally Separated Data Sets Reveal Similar Traits of Birds Persisting in a United States Megacity* by Cooper et al. analyzes life history and behavioral traits associated with urbanization for 52 breeding bird species on 173 survey blocks in the Los Angeles area of southern California, United States, in the late 1990s and again in the 2010s. This study finds that cavity-nesting and migratory behavior are filters that prevent successful persistence in urban areas as they are negatively associated with urbanization, and nesting on human-made structures is positively associated with urbanization. Winandy et al. assess how *urban noise restricts song frequency bandwidth and syllable diversity in bananaquits: increasing audibility at the expense of signal quality* and imply negative consequences in terms of sexual selection for reduced signal quality. Winandy et al. *Noise-Related Song Variation Affects Communication: Bananaquits Adjust Vocally to Playback of Elaborate or Simple Songs* nicely complements their other paper with playback experiments to reveal that songs with reduced syllable diversity and bandwidth receive weaker responses from territorial rivals, thus have an associated cost in terms of sexual selection. Phillips et al. find evidence that *Territory Quality Predicts Avian Vocal Performance Across an Urban-Rural Gradient.* The pattern of association between vocal performance, vegetation characteristics, and ambient noise levels, provides intriguing insights and raises new questions about the underlying mechanisms driving variation in song performance. In their paper *Incubation Behavior Differences in Urban and Rural House Wrens, Troglodytes aedon* Heppner and Ouyang find that urban females spend less time incubating, and have more and shorter incubation bouts, in association with higher ambient temperatures than rural females, which could be a consequence of the urban heat island effect.

While the aforementioned papers explore previously known urban phenotypes, several papers in this issue investigate which aspects of the urban environment organize urban communities and their spatial orientation within cities. *Vigilance Response of a Key Prey Species to Anthropogenic and Natural Threats in Detroit* by Lima et al. find that urban rabbits are most vigilant in areas with high domestic dog activity and that they avoid areas with carnivores such as coyotes. Meanwhile Hansen et al. explore the fundamental ecological relationship of habitat productivity and species distributions but do so within the confines of an urban area. *Does Use of Backyard Resources Explain the Abundance of Urban Wildlife* quantifies the relative influence of anthropogenic resources (food, water, shelter) in residential yards on the relative abundance of mammals. They find that food resources are an attractant of mammals to yards and predator species are associated with the relative abundance of mammalian prey species in those yards.

Finally, a few papers in this issue take a step back for a larger view of how animals are adapting to urban habitats with systematic reviews of the adaptations of mammals and of lizards to life in the city. *Behavior Change in Urban Mammals: A Systematic Review* by Ritzel and Gallo present a systematic review of literature regarding urban mammal behavior over the last 50 years. They identify taxonomic, regional, and behavioral biases in the literature and discuss the adaptive responses (regulatory, acclimatory, and developmental) of mammals to urbanization. Putman and Tippie's *Big City Living: A Global Meta-Analysis Reveals Positive Impact of Urbanization on Body Size in Lizards* provides a systematic review of the different selective pressures in urban environments compared to natural environments and how they lead to changes in animal behavior, physiology, and morphology among lizards. Lizards living in urban environments are larger than rural lizards and urban lizards use larger perches and have longer hind limbs. In the theme of stepping back and seeing the bigger picture of the urban phenotype, Halfwerk presents an opinion piece entitled *How Should We Study Urban Speciation,* in which he provides a candid perspective that illustrates our current lack evidence to fully assess speciation in urban environments. Lailvaux also takes a big picture approach to the urban phenotype by reviewing the different selective pressures on urban as compared to rural green Anole lizards and using long-term mark recapture experiments to assess sex-ratios and population density in urban environments. Lailvaux's *It's Not Easy Being Green: Behavior, Morphology, and Population Structure in Urban and Natural Populations of Green Anole (Anolis carolinensis) Lizards* finds that urban and rural lizards have diverged significantly in terms of their behavior and morphology.

While this special issue shines light on the urban phenotype, and several of the environmental mechanisms that lead to their divergence from rural populations, many questions remain unanswered. The largest of which is that we don't know the extent to which divergence among urban and rural populations leads to fitness consequences, or even to genotypic changes. This issue advances our understanding of the urban phenotype while also highlighting the continued need for research on whether urban adaptations have led to meaningful divergence from rural populations.

AUTHOR CONTRIBUTIONS

DL and ED conceived, wrote, edited, and approved of the submission of this editorial article. All authors contributed to the article and approved the submitted version.

REFERENCES

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., et al. (2008). Global change and the ecology of cities. *Science* 319, 756–760. doi: 10.1126/science.1150195

Isaksson, C., and Andersson, S. (2007). Carotenoid diet and nestling provisioning in urban and rural great tits (*Parus major*). *J. Avian Biol.* 38, 564–572. doi: 10.1111/j.0908-8857.2007.04030.x

Narango, D. L., Tallamy, D. W., and Marra, P. P. (2017). Native plants improve breeding and foraging habitat for an insectivorous bird. *Biol. Conserv.* 213, 42–50. doi: 10.1016/j.biocon.2017.06.029

Plumptre, A. J., Baisero, D., Belote, R. T., Vázquez-Domínguez, E., Faurby, S., et al. (2021). Where might we find ecologically intact communities? *Front. For. Glob. Change* 4:26. doi: 10.3389/ffgc.2021.626635

Putman, B. J., Gasca, M., Blumstein, D. T., and Pauly, G. B. (2019). Downsizing for downtown: limb lengths, toe lengths, and scale counts decrease with urbanization in western fence lizards (*Sceloporus occidentalis*). *Urban Ecosyst.* 22, 1071–1081. doi: 10.1007/s11252-019-00889-z

Rivkin, L. R., Santangelo, J. S., Alberti, M., Aronson, M. F., de Keyzer, C. W., Diamond, S. E., et al. (2019). A roadmap for urban evolutionary ecology. *Evolut. Appl.* 12, 384–398. doi: 10.1111/eva.12734

Seress, G., Hammer, T., Bókony, V., Vincze, E., Preiszner, B., Pipoly, I., et al. (2018). Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. *Ecol. Appl.* 28, 1143–1156. doi: 10.1002/eap.1730

Seto, K. C., Güneralp, B., and Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. U.S.A.* 109, 16083–16088. doi: 10.1073/pnas.1211658109

Sparkman, A., Howe, S., Hynes, S., Hobbs, B., and Handal, K. (2018). Parallel behavioral and morphological divergence in fence lizards on two college campuses. *PLoS ONE* 13:e0191800. doi: 10.1371/journal.pone.0191800

Swaddle, J. P., Francis, C. D., Barber, J. R., Cooper, C. B., Kyba, C. C. M., Dominoni, D. M., et al. (2015). A framework to assess evolutionary responses to anthropogenic light and sound. *Trends Ecol. Evolut.* 30, 550–560. doi: 10.1016/j.tree.2015.06.009

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ORIGINAL RESEARCH
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Variation in Diurnal Patterns of Singing Activity Between Urban and Rural Great Tits

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Human settlements and activities alter the natural environment acoustically and visually. Traffic noise and street lights are two of the most prominent pollutants which may affect animal activity patterns. Birds in urban areas have been reported to sing nocturnally and to have an earlier dawn chorus compared to their rural counterparts. However, few studies have measured whether singing more at night or earlier in the morning means singing less during daytime. It is therefore unclear whether they shift or extend or overall increase their activities. Furthermore, few studies on anthropogenic noise-related shifts in song activity replicated well at the habitat level. We recorded singing activity in urban and rural great tits (*Parus major*) for 24 h and sampled 11 urban–rural pairs of territories, inside and outside 11 different cities across the Netherlands. We found that urban birds sing earlier during the day, have similar singing effort in the dawn chorus, but sing less than rural birds during the rest of the day. The shift in timing between urban and rural birds was 22 min on average and resulted in more songs for urban birds during a less noisy time of the day. The lower singing activity over the day made that urban birds sang less when it was more noisy compared to the natural rhythm of rural great tits. We currently lack insight into whether these differences yield any positive or negative fitness consequences, but it is a clear case of how anthropogenic effects on the natural environment influence fundamental aspects of daily life in the animal communities with which we share the urban habitat.

Keywords: birdsong, dawn chorus, diurnal patterns, traffic noise, temporal shift

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INTRODUCTION

Activity patterns are species-specific, typically driven by natural environmental and social cues (Aide et al., 2013; Frey et al., 2017), but can be affected by human disturbance (Barrueto et al., 2014; Lendrum et al., 2017; Gaynor et al., 2018). Some species are diurnal, others nocturnal, and many have crepuscular peaks of activity around dawn or dusk. These labels are typically based on activity biases in foraging, nest building, or moving around, but may also apply to preference period for vocal activity. Many mammals are naturally most active at night (Frey et al., 2017; Ogurtsov et al., 2018), but there are also reports on species that are diurnal in undisturbed areas and nocturnal where human are active or noisy during daytime (e.g., Martin et al., 2010; Marchand et al., 2014). Many species of birds peak in singing activity around dawn and in the morning (Bruni et al., 2014; Pérez-Granados et al., 2018), but also here urban species have been reported to be active at night and wake up earlier due to daytime noise pollution (Fuller et al., 2007; Dominoni et al., 2013; Swaddle et al., 2015). However, the nature of this shift is still not well understood as few studies on avian vocal activity patterns replicated well at the level of the habitat and few studies collected detailed data across the 24 h of a full day.

Most birds are more active during the day than during the night and often have a distinct peak in singing activity around dawn (Aide et al., 2013; Bruni et al., 2014; Pérez-Granados et al., 2018). Explanations for this activity bias to this early hour include coinciding peaks in female fertility and competitor risk, optimal air conditions for sound transmission, and low foraging profitability related to inadequate light conditions (Kacelnik and Krebs, 1983; Mace, 1987; Brown and Handford, 2003). Variation among species must be related to variation in species-specific physiology or sensory capacity, which would render a different trade-off among activities such as foraging and singing. Variation in timing does not only occur among species, but also within species. Seasonal variation, in particular in temperate zones, is driven by hormonal cycles related to the breeding season (Nottebohm, 1981; Ball, 1999), but also weather and habitat may affect singing effort and timing.

Natural variation in ambient noise and light conditions are known to affect singing activity and to explain variation in activity patterns among days. Cicada calling can be loud, in particular in tropical areas, and may drive bird species that overlap in song frequency use to adjust their timing (Hart et al., 2015). This is also the explanation for why high-frequency singing bird species rise later than low-frequency singers in tropical forests with intense nighttime cicada chorusing at high frequencies (Stanley et al., 2016). Birds in the temperate zone of rural North America were reported to sing earlier with full or third-quarter moon, which makes light levels to be higher at dawn (Bruni et al., 2014). An opposite effect has been found in temperate zones of both North-America and Europe for birds that delayed their dawn chorus and stopped singing earlier at dusk with cloud cover and rain, which obviously dims the light levels (Nordt and Klenke, 2013; Bruni et al., 2014; Da Silva et al., 2014). Understorey and canopy birds of tropical forests may even also exhibit light-level-related differences in vocal activity patterns (Blake, 1992; Berg et al., 2006).

The presence of human settlements and infrastructure can also alter environmental cues and make urban and rural birds of the same species wake up at different times (Bergen and Abs, 1997; Swaddle et al., 2015). Typically, urban birds are active earlier in the day and in the season compared to rural counterparts (Miller, 2006; Da Silva et al., 2015). Sometimes, differences in the morning are followed by differences in the rest of the day: short or disturbed nights may be compensated with a nap (Raap et al., 2016) or with just lower activity levels during daytime (de Jong et al., 2016). This may yield further divergence in daily activity patterns between birds of different habitats. Cartwright et al. (2014), for example, conducted a study with long-term passive recordings at three high-traffic and two low-traffic sites in southern Ontario, Canada. They found that red-winged blackbirds (*Agelaius phoeniceus*) sang more at dawn and dusk at the rural sites and more during midday at the urban sites. Traffic noise and street lightening are two of the most prominent pollutants that are put forward as causing such divergence in avian rhythms (Nordt and Klenke, 2013; Lee et al., 2017), with sometimes sound put forward as most prominent factor (e.g., Fuller et al., 2007) and sometimes light (e.g., Da Silva et al., 2014).

Great tits are a great model system to study vocal variation and habitat-dependent song activity patterns. Males are highly vocal during the breeding season (Garson and Hunter, 1979), and they use distinct song types that are typically well contrasting with other songbird songs and known to play a role in territory defense and mate attraction (Krebs et al., 1978; Mace, 1987; Slagsvold et al., 1994). They occur in both urban and rural areas and typically sing close to their nest, which is often a nest box (e.g., Halfwerk et al., 2011, 2012). Such artificial nesting opportunities are usually easy to localize and are numerous in urban areas, but people also tend to provide them in many rural areas (e.g., at relatively isolated houses and farms, in recreational woodlands, on campings and holiday home parks, and in special study populations dedicated to scientific research). Great tits were also the model species in some of the early papers on habitat-dependent song variation (Hunter and Krebs, 1979; Bergman, 1982; Lehtonen, 1983) and have been studied intensively for urban–rural comparisons (e.g., Slabbekoorn and den Boer-Visser, 2006; Slabbekoorn and Ripmeester, 2008; Mockford and Marshall, 2009; Senar et al., 2017; Caorsi et al., 2019; Ulgezen et al., 2019). However, we still lack a well-replicated urban-rural comparison in great tits on the timing and amount of singing during the dawn chorus and the rest of the entire day.

In the current study, we recorded 24-h song activity cycles of a replicated set of individual great tits, in a paired sampling design. We recorded 11 pairs of territorial male birds, with each pair sampled during the same 24-h period, and consisting of an urban territory, with city noise and light conditions, and a more quiet and dark territory in a nearby rural woodland area. Pairs of birds were sampled in different cities across an area of 150 by 150 km, from The Hague to Nijmegen and Amsterdam to the Belgian border. We aimed to answer the following questions: (1) Do urban great tits indeed sing earlier than nearby rural great tits? (2) Do urban great tits sing more or less, and shorter or longer, during the dawn chorus and more or less over the rest of the day after the dawn chorus? and (3) If there are differences in timing or amount of singing, can they be related to noise avoidance: Do great tits avoid singing during the most noisy times of the day? We expected that urban great tits would sing earlier than rural great tits. They may also stop earlier with the dawn chorus and sing less, which they may compensate by singing more the rest of the day. Alternatively, they may also show an effect of elevated competition for acoustic space by traffic noise during the rest of the day and sing less than their rural counterparts.

MATERIALS AND METHODS

Study Sites and Passive Recording Approach

This study was conducted from March to May of 2017 in 11 pairs of sampling sites, inside (urban) and outside (rural) 11

FIGURE 1 | Map with the locations of the 11 urban and rural pairs inside and outside main cities across the Netherlands. The black symbols represent the urban sites and the green symbols represent the rural sites. The red circles indicate the cities, with size reflecting relative size. We also show the image of the automatic recorders (Song Meter SM1) used to conduct our 24-h recordings.

cities across the Netherlands (**Figure 1**). In each of nine urban–rural pairs of sites, including the large cities (Dutch standards) of Amsterdam, Rotterdam, and The Hague, we sampled a great tit territory, well inside built-up areas at a relatively noisy place. A great tit territory away from houses and streets in woodland area, selected for being relatively quiet, was sampled in a random direction, ∼15–30 km apart from the urban site. Two urban-rural sites, Utrecht and Leidsche Rijn, were adjacent to each other, concerning historical old town and new residential areas, respectively, for which we sampled a matching rural site in woodland area east from Utrecht (see **Figure 1**). Recordings within a pair of urban and rural sites were conducted synchronously on the very same day, while sampling of pairs were scattered through the season (**Table 1**).

In each of the 22 sampling sites, we selected a great tit male prominently advertising territory ownership by singing near a nest box. After the selection of the focal male, we observed the song posts defining his territory and we identified the boundaries of that territory. We recorded song activity for one cycle of 24 h for each great tit male with an automatic recorder (Song Meter SM1, Wildlife Acoustics Inc., Concorde, MA, United States, sample rate 44.1 kHz, 16-bits, stereo; see **Figure 1**). We placed

TABLE 1 | Urban and rural pairs of sites and information about the date of recording, sunrise time (from https://cdn.knmi.nl), dawn chorus start, end and duration time, sunset time, last song of the daytime and total singing time.

Site	Urban/Rural	Date	Sunrise Time	Dawn chorus			Sunset Time	Last song of the day	Total Singing
				Start	End	Duration			
Arnhem	Urban	01-Apr	7:11	5:33	7:00	1:26	20:26		
Arnhem	Rural	01-Apr	7:11	6:23	7:07	0:44	20:26		
Bergen op Zoom	Urban	04-Apr	7:11	5:46	6:10	0:24	20:21	20:13	14:27
Bergen op Zoom	Rural	04-Apr	7:11	6:28	8:27	1:59	20:21	20:17	13:48
Rotterdam	Urban	08-Apr	7:01	5:32	8:05	2:32	20:28	20:09	14:36
Rotterdam	Rural	08-Apr	7:01	5:43	6:52	1:08	20:28	20:25	14:42
Amsterdam	Urban	11-Apr	6:52	5:57	7:01	1:04	20:32	19:52	13:55
Amsterdam	Rural	11-Apr	6:52	6:14	7:04	0:50	20:32	19:57	13:43
Utrecht	Urban	19-Apr	6:34	5:30	6:24	0:54	20:44	17:18	11:48
Utrecht	Rural	19-Apr	6:34	5:53	7:03	1:09	20:44	20:06	14:13
Leidsche Rijn	Urban	20-Apr	6:32	5:22	5:34	0:11	20:46	13:05	7:42
Leidsche Rijn	Rural	20-Apr	6:32	5:46	6:52	1:05	20:46	19:59	14:12
Schaijk	Urban	24-Apr	6:22	5:43	6:43	1:00	20:50	20:02	14:19
Schaijk	Rural	24-Apr	6:22	5:44	6:21	0:36	20:50	20:19	14:34
Hilversum	Urban	27-Apr	6:17	5:37	6:14	0:36	20:24	19:58	14:20
Hilversum	Rural	27-Apr	6:17	5:38	6:42	1:03	20:24	20:25	14:47
The Hague	Urban	30-Apr	6:15	4:50	6:10	1:19	21:06	20:44	15:53
The Hague	Rural	30-Apr	6:15	5:34	6:32	0:57	21:06	19:58	14:24
Nijmegen	Urban	03-May	6:04	5:05	6:22	1:17	21:04	20:52	15:46
Nijmegen	Rural	03-May	6:04	5:45	6:13	0:28	21:04	20:23	14:38
Leiden	Urban	16-May	5:46	4:53	5:55	1:01	21:32	20:51	15:57
Leiden	Rural	16-May	5:46	4:59	5:56	0:56	21:32	19:34	14:34

Time is displayed in hours and minutes.

the recorder on a song post close to the nest box of the male great tit, which guaranteed high-quality recordings, as male tits sing close and often toward the nest box, prior to and during breeding activity (see Halfwerk et al., 2011, 2012). The automatic recorders were programmed to record a sequence of 24 1-h recordings. Ending one recording and starting a following one, lasted 30 s. We, therefore, miss data for a very short period every hour (0.8%), and we had to take a shift into account of accumulating 30 s periods over the day, when attributing song activity to a particular hour slot. The Song Meters were placed during daytime, but all recordings started at 3:30 in the night. In one of the 22 sites, the city of Arnhem, our recording had stopped at 11:30 in the morning (well after the dawn chorus) for unknown reasons, and for some of the analyses, we therefore had to drop this pair of sites.

Timing and Amount of Singing

We used spectrograms generated in Avisoft-SASLab Lite 5.2.10 (sample rate 44.1 kHz, sample size 16-bits, FFT length = 256 points, frame size 100%, overlap 75%, frequency resolution 172 Hz, temporal resolution 1.45 ms, Hamming window) to determine the timing and amount of singing of great tits during the 24-h cycles. We defined the start, duration and end of the dawn chorus for each male, as well as the last song of the day and the total singing time (**Table 1**). The start of the dawn chorus was simply the first song detected in our recordings. The end of the dawn chorus was determined by measuring song intervals: it was considered the end of the dawn chorus when a bird had not sung for longer than 7 min. In a study by Naguib et al. (2019), 98% of the inter-song intervals during the dawn chorus singing, before sunrise, were shorter than 7 min, which was the reason to take this interval length as the end of dawn chorus criterion (c.f. Naguib et al., 2019). We expressed start and end times also relative to sunrise or sunset to allow comparisons across the season (**Table 1**). Furthermore, we counted the number of songs of the focal male every hour. Great tit males have small repertoires, around 2–6 types in our sample, and repeat the same song type for several minutes before they switch to a different song type (Halfwerk et al., 2012). The discrete nature of great tit song types further helped to extract target songs from the background with other songs from other species, and potentially further-away neighbors. Although focal males also moved around among different singing perches, and song amplitude on the recording varied accordingly, we rarely had any difficulty in distinguishing focal male song and faint songs of distant neighbors.

Noise Measurements and Fluctuation Patterns

We assessed the short-term amplitude levels of the background noise at each site, using a Voltcraft SL-100 sound level meter (range, 30–130 dB; A-weighting, fast response). All sites were measured once, associated with installing or collecting the Song Meter and thus associated with the paired assessment of singing activity throughout the season. All measurements were taken between 6:00 and 13:00 h, except for one pair of sites, which was measured late in the afternoon (see **Table 2**). We measured noise levels for 5 min: 1 min in each of the five directions (north, east, south, west, and up). During 1 min, we recorded the highest amount of noise every 10 s (6 measurements per minute). Noise levels were averaged for each site. In addition, we analyzed the long-term noise fluctuations in each territory using our passive recordings from the Song Meters.

We analyzed relative noise fluctuations in time, using the long-term recordings, in two frequency bands: a low band between 200 and 400 Hz and a high band between 2000 and 4000 Hz. The lower band reflects traffic activity well, as there are very few birds making sound below 400 Hz and traffic noise is biased toward low frequencies (Slabbekoorn and Peet, 2003). The high band reflects bird song activity, including the frequency range of the songs of great tits and excluding a major contribution from traffic noise. For each frequency band, we selected the highest amplitude in periods of 1 min using a power spectrum (FFT length: 256 points, window type: Hamming) generated in Avisoft-SASLab Lite 5.2.10. To assess fluctuations in time, we took three of such 1 min amplitude measurements per hour. These three measurements were taken in three different time blocks within the hour: (1) from 0 to 20 min, (2) from 20 to 40 min, and (3) 40–60 min. We avoided songs from our focal great tit male in the one-min selections, and, when his dawn chorus singing was very dense, we occasionally merged separate periods from the same time block into a one-min composite selection. We averaged the three samples to get a single amplitude measure per hour. We determined relative noise level for each hour per territory by subtracting the hourly averages from the overall average of the day.

We assessed spectral differences in the ambient noise between urban and rural sites to provide the context of potential masking by spectral overlap that could drive the temporal patterns explored in our analyses. We used 20 one-min samples from our urban and rural sites, excluding songs from the focal bird, but taken from the morning hour with most singing activity (5.30–6.30) (**Figure 2**). Urban sites have relatively high amplitude levels in the low frequencies (<3000 Hz) in comparison to rural sites, and relatively low amplitude levels for high frequencies (>3000 Hz). These patterns reflect the prominent presence of traffic noise in urban sites (low frequencies) and more prominent presence of singing birds (high frequencies) in rural sites, which is in line with many other reports (e.g., Slabbekoorn and Peet, 2003; Pohl et al., 2009; Nemeth and Brumm, 2010).

TABLE 2 | Times and dates for when short-term noise measurements were taken for each of the pairs of rural and urban sites.

	Times and dates short-term noise measurements			
Site	**Rural**	**Date**	**Urban**	**Date**
Arnhem	17:02	02-Apr	10:19	02-Apr
Bergen op zoom	06:24	05-Apr	08:09	05-Apr
Rotterdam	06:50	13-Apr	08:24	09-Apr
Amsterdam	08:40	12-Apr	06:50	12-Apr
Utrecht	06:23	20-Apr	10:09	20-Apr
Leidsche Rijn	07:10	21-Apr	10:35	21-Apr
Schaijk	08:45	25-Apr	06:08	25-Apr
Hilversum	10:56	28-Apr	07:48	28-Apr
The Hague	10:20	01-May	10:48	29-Apr
Nijmegen	11:17	04-May	14:59	04-May
Leiden	11:39	15-May	12:35	17-May

Statistical Analyses

We conducted all statistical analyses in R version 3.5.1 (R Core Team, 2019). To investigate if the timing of singing was different between urban and rural great tit males, we compared the start, end and duration of the dawn chorus, last song of the day and total singing time. We performed an Exact Permutation test for dependent samples stratified by site in the R Coin package (Hothorn et al., 2008). We also conducted an Exact Permutation test for dependent samples stratified by site to compare the amount of singing between urban and rural males comparing number of songs sang during the dawn chorus, during the rest of the day and during each hour of the day. Furthermore to assess potential differences between rural and urban relative noise levels of low- and high-frequency bands for each hour of the day, we performed another Exact Permutation test stratified by site. The Exact Permutation tests allow deviation from a normal distribution, which was often the case for our variables (except for start relative to sunrise, number of songs during dawn chorus and some relative noise levels for certain hours). In order to analyze if the noise levels of the low- and high-frequency bands had an impact on the amount of singing, we used a Spearman's rank correlation test or Pearson's correlation test when the data were normally distributed. We correlated the number of songs and the amplitude levels relative to the noise average of the day for each site and each frequency band.

RESULTS

Timing of the Dawn Chorus

We analyzed a total of 513 h of recordings from 22 male great tits in 11 urban–rural pairs of sites. Urban great tits started to sing significantly earlier in the morning than rural great tits (mean ± SE; Urban: 66 ± 6.04, range: 39–97 min before sunrise; Rural: 45 ± 4.63, range: 19–78 min before sunrise; z = -2.56, p < 0.001, Exact Permutation test; **Figure 3A** and **Table 1**). The average difference of 22 min was reflecting a persistent earlier start in the city throughout the season, although the difference varied substantially between about the same starting time up to a 50 min difference (**Figure 3C**). The duration of the dawn chorus and the end of the dawn chorus relative to sunrise were not significantly different between urban and rural birds (mean ± SE; Duration, Urban: 64 ± 11.26, range: 12–153 min; Rural: 58 ± 7.23, range: 29–119 min; z = -0.44, p = 0.68, Exact Permutation test; **Figure 3B**; End, Urban: -1 ± 10.60, range: -60 to 65 min; Rural: 17 ± 6.93, range: -9 to 77 min; z = 1.11, p = 0.30, Exact Permutation test; **Table 1**). Note that differences in dawn chorus start were more consistent than duration differences, the

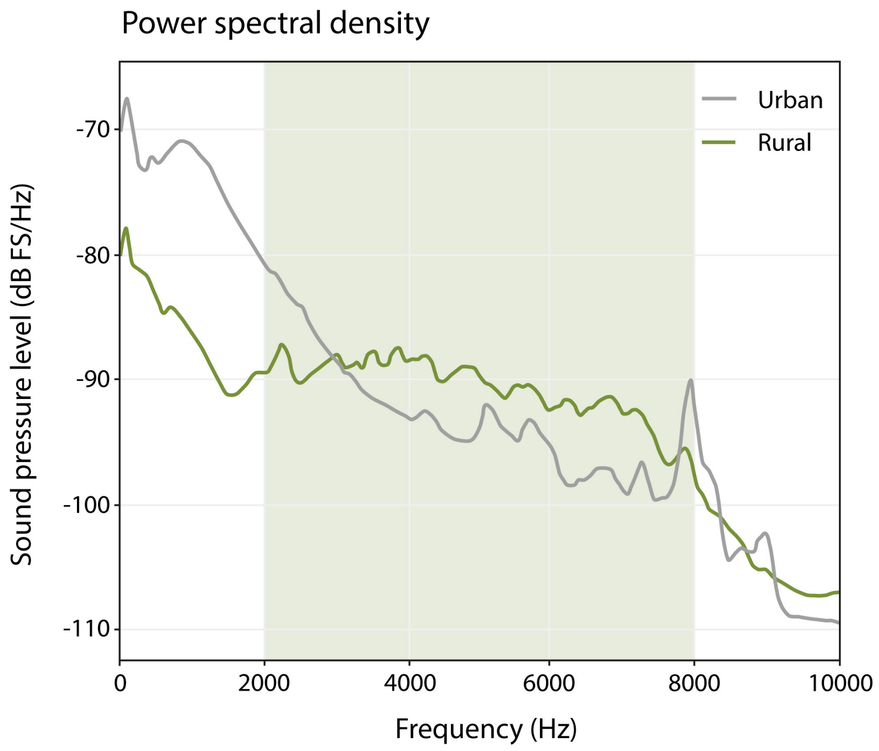

FIGURE 2 | Power spectral density plot (window length: 512, window type: Hann) of urban and rural sites, based on the average of 10 one-min samples for urban sites, and 10 one-min samples for rural sites, during the morning hour with most singing activity (5:30–6:30). The green-shaded area represents the frequency range used by great tits between 2000 and 8000 Hz. Note that below 3000 Hz, urban great tits have relatively more competition for acoustic space than rural birds, and above 3000 Hz, rural birds have a relatively more noisy background.

latter of which were also more variable, for example ranging from 20 min until 160 min for urban birds (**Figure 3B**). The time of the last song of the day relative to sunset and the total time singing during the 24 h were also not significantly different between urban and rural great tits (mean ± SE; Last song: Urban: 140 ± 95.02, range: 8–979 min; Rural: 38 ± 11.27, range: −2 to 118 min; $z = -1.07$, $p = 0.38$, Exact Permutation test; Total singing: Urban: 833 ± 47.18, range: 462–958 min; Rural: 862 ± 6.98, range: 823–887 min; $z = 0.66$; $p = 0.51$, Exact Permutation test; **Table 1**). The earliest song recorded was at 4:50 and the latest song was at 20:55 (**Table 1**), while we did not hear any songs recorded during nighttime.

Amount of Singing Activity Over the Day

We found that the numbers of songs sung by urban and rural great tits during the dawn chorus were not significantly different (mean ± SE; Urban: 274 ± 48.83, range: 25–526 songs; Rural: 322 ± 47.74, range: 126–638 songs; $z = 0.55$, $p = 0.61$, Exact Permutation test; **Figure 4A**). In contrast to that, urban great tits sang significantly less songs than rural great tits during the rest of the day (mean ± SE; Urban: 567 ± 84.77, range: 127–988 songs; Rural: 1058 ± 174.42, range: 460–2258 songs; $z = 2.13$, $p = 0.03$, Exact Permutation test; **Figure 4B**). We found more songs sung by rural than by urban birds for more than half of the 17 h of the day. At the hours starting at 4:30, 7:30, 9:30, 10:30, 12:30 to15:30 and 17:30 to 18:30, we found either a significant difference or a non-significant trend ($p < 0.05$ and $p = 0.06$–0.08, respectively; Exact Permutation test; **Figure 4C**).

Noise Levels and Fluctuations Over the Day

The average noise levels, determined by 22 sets of peak level assessments, using the sound level meter (short-term noise measurements), were significantly higher for territories in urban than for territories in rural sites (mean ± SE, $n = 11$, Urban: 53.6 ± 1.9 dB; Rural: 45.9 ± 1.3 dB; Exact Permutation test; $z = -2.41$; $p = 0.01$). We also found significant differences or non-significant trends ($p < 0.05$ and $p = 0.06$–0.08, respectively; Exact Permutation test) for certain hours in the fluctuating patterns over the day between urban and rural sites for both, the low- and high-frequency bands (**Figures 5A,B**), through 1,440 one-min measurements on the Song Meter data (long-term noise measurements). From a more general perspective, the low-frequency band (200–400 Hz), reflecting traffic noise, exhibited relatively high levels (above the noise average of the day) between 5:30 and 22:30, while it was relatively quiet (below the noise average of the day) between 00:30 and 4:30 (see **Figure 5B**). Although this pattern was generally true for both urban and rural sites, rural sites were relatively less quiet

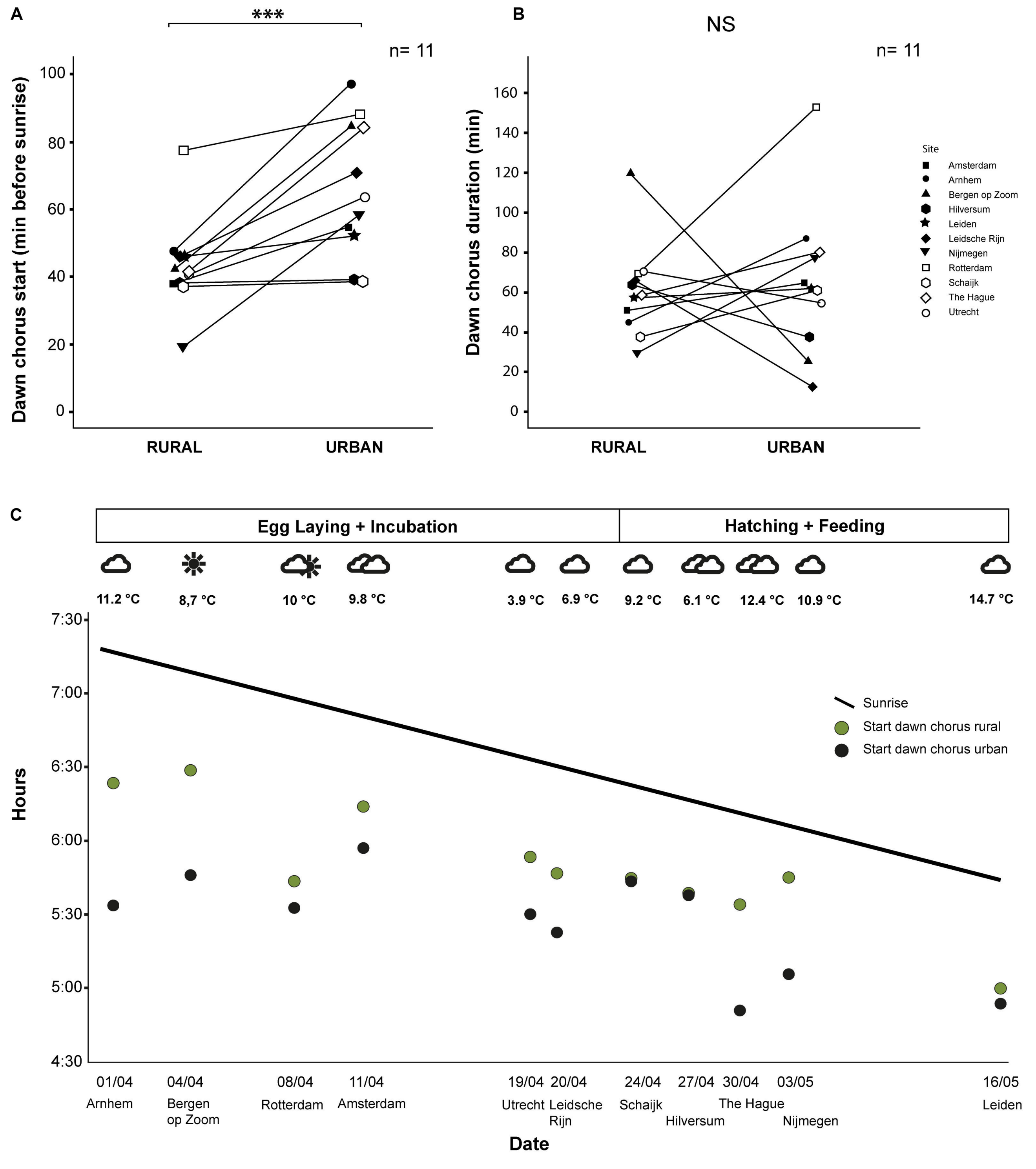

FIGURE 3 | Timing of singing for urban and rural great tits: **(A)** Dawn chorus start time relative to sunrise (*** means a significant difference at $p < 0.001$ level); **(B)** Duration of the dawn chorus (NS means not significant); and **(C)** Seasonal change of the start of the dawn chorus (line reflects changing sunrise). We indicated breeding phase and weather conditions for the sampling dates at the top and sampling date and pair location (by city name) at the bottom. See text for statistics.

during the night and early morning than urban sites (between 00:30 and 7:30), while urban sites were relatively more noisy in the late afternoon than rural sites (between 16:30 and 20:30). The high-frequency band (2000–4000 Hz), reflecting general bird singing activity, was relatively high for both habitat types throughout the daytime (5:30–20:30), with highest levels as

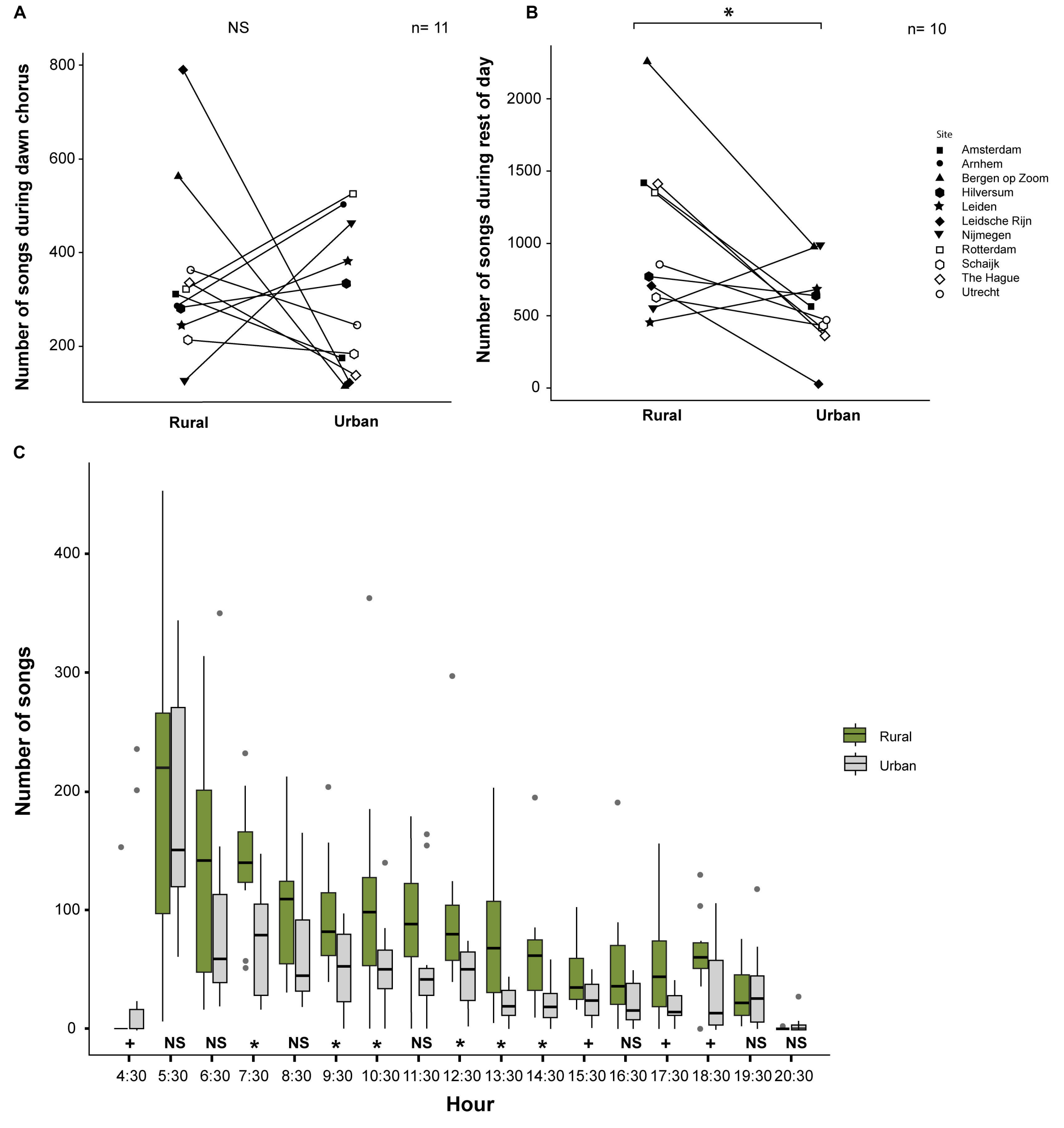

FIGURE 4 | Amount of singing for urban and rural great tits: **(A)** Number of songs during the dawn chorus (NS means not significant); **(B)** Number of songs during the rest of the day (* means a significant difference at $p < 0.05$ level); and **(C)** Number of songs per hour for both urban and rural sites (Diurnal pattern, * means a significant difference between the habitats at $p < 0.05$ level and + means a non-significant trend). See text for statistics.

expected during the dawn (5:30–7:30) and dusk chorus (18:30–20:30; **Figure 5A**).

Covariation Between Noise Level and Singing Activity

In addition to the previous description of the general noise patterns between rural and urban sites, we also analyzed the singing activity of the great tits in relation to the noise level fluctuations over the 24 h of a day. By starting to sing 22 min earlier, on average throughout the season, up to occasionally 50 min (around 5:30 or even earlier, late in the season), urban birds do shift singing activity into a relatively more quiet time period of the day. However, there were no significant differences in the amount of singing between birds in both habitats during

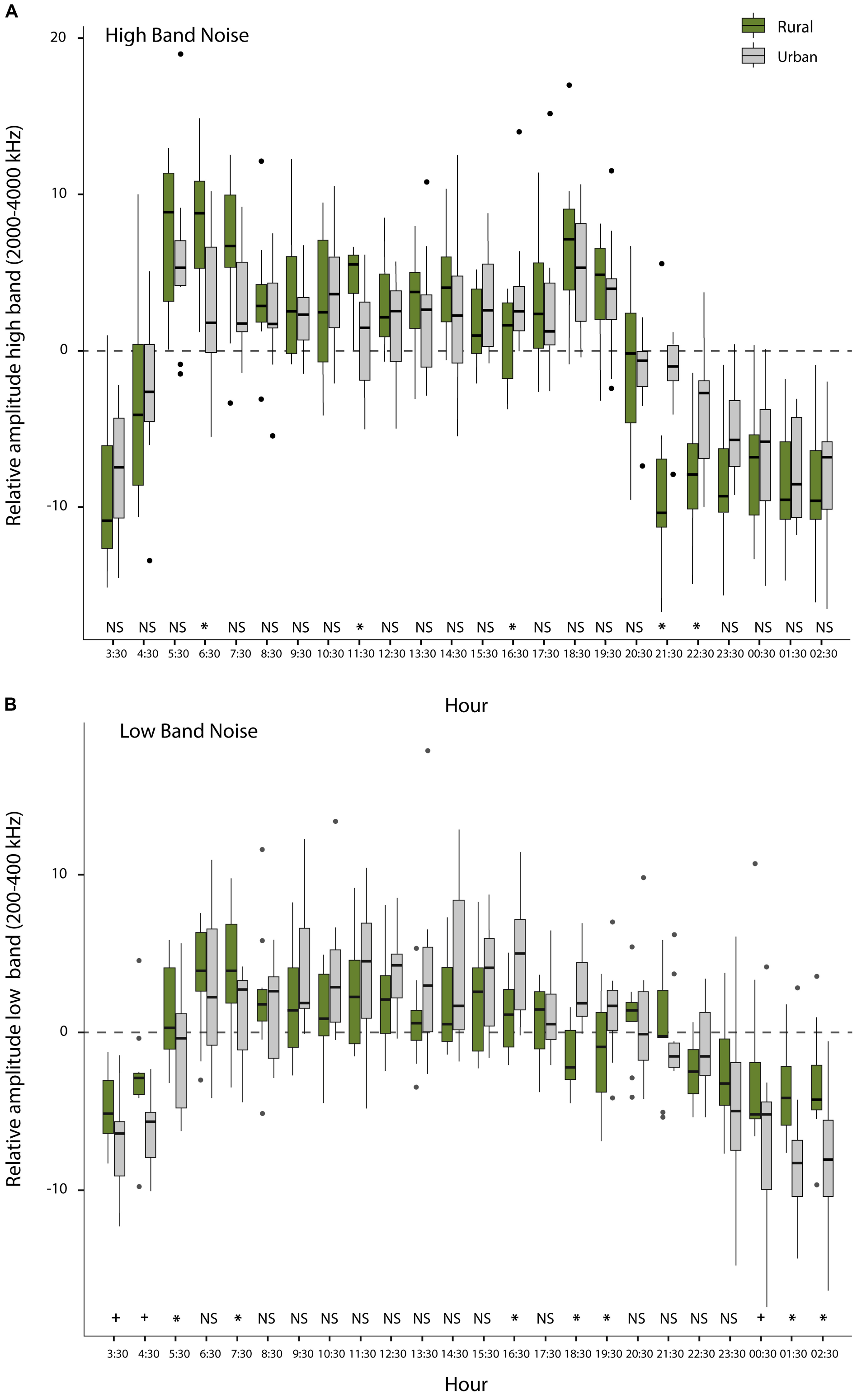

FIGURE 5 | Relative noise level fluctuations over the day: **(A)** Average noise level per hour subtracted from the overall mean of the day (represented with the zero value) for each habitat for the high-frequency band (2000–4000 Hz), reflecting fluctuations in local bird song activity other than that of the focal great tits; **(B)** Average noise level per hour subtracted from the overall mean of the day (represented with the zero value) for each habitat for the low-frequency band (200–400 Hz), reflecting local fluctuations caused by traffic noise (* indicates a significant difference at $p < 0.05$ level and + means a non-significant trend). See text for statistics. The dashed line illustrates the overall noise of the day.

those early hours (**Figures 4C**, **5B**). Nevertheless, urban birds sang often less than rural birds later in the morning and in several afternoon time blocks, when urban noise levels were higher than at 5:30 (**Figures 4C**, **5B**). We found an overall significantly positive correlation between the number of songs sung and the level of background noise of the low- and high-frequency bands, for both urban and rural sites (see results in **Table 3** and **Figures 6A–D**). These correlations are driven and can be explained by the fact that: (1) during the 24 h analyzed, the quietest moments of the day, at night, are when birds are not singing; and (2) the loudest moments due to rush hours or overall high vocal activity by birds were also singing peaks for great tits. Removing the night hours from this analysis would remove many of the site-specific significant correlations: from 11 to 3 out of 20 for the low-frequency band and from 16 to 6 out of 20 for the high-frequency band (see **Table 3**).

DISCUSSION

We were able to show distinct differences in timing and amount of singing between urban and rural great tits in a well replicated and paired set of passive audio recordings of 24 h. We found the following answers to our questions: (1) Urban great tits indeed sang earlier than nearby rural great tits; (2) Urban great tits did not sing more or for longer in the dawn chorus, but sang significantly less than rural birds over the rest of the day; and (3) Starting 22 mins earlier on average, up to 50 min, in urban relative to nearby rural territories on the same day, resulted in more songs in a less noisy time of the day for city birds. However, in general great tits do not seem to avoid singing during the most noisy times of the day, as song activity level was positively correlated to relative ambient noise levels in the low-frequency band of 200–400 Hz, which is a good monitor of traffic noise.

Patterns and Processes

We were able to confirm what has been found in many studies: urban birds start singing earlier than rural birds (Bergen and Abs, 1997; Swaddle et al., 2015; Da Silva and Kempenaers, 2017). This pattern is not only known from cities, but has also been reported repeatedly for airports (Gil et al., 2015; Dominoni et al., 2016; Sierro et al., 2017). Our study is the first with a proper replication at the level of the habitat, with sampling of 11 urban–rural territories across the Netherlands. We also recorded a full 24-h cycle, which allowed us to analyze whether early morning adjustments concern a shift or extension of their active period. We were therefore able to show that urban birds started earlier, but that this does not affected how much they sang in the same hour bins during the dawn chorus compared to rural birds. The dawn chorus duration of urban great tits was also not significantly

TABLE 3 | Correlations between number of songs and noise amplitude levels relative to the noise average of the day, for each site (urban and rural) and for each frequency band (low band noise: 200–400 Hz; high band noise: 2000–4000 Hz).

		24 h, including night hours				**Excluding night hours**			
Site	**Urban/ Rural**	**Low band noise**		**High band noise**		**Low band noise**		**High band noise**	
		R	**p**	**R**	**p**	**R**	**p**	**R**	**p**
Bergen op Zoom	Urban	**0.76**	**<0.001**	**0.67**	**<0.001**	0.063[a]	0.82	**–0.19[a]**	**0.047**
Bergen op Zoom	Rural	–0.14	0.51	**0.86**	**<0.001**	–0.064[a]	0.82	**0.54[a]**	**0.037**
Rotterdam	Urban	–0.3	0.16	**0.49**	**0.015**	**–0.66**	**0.007**	0.18	0.52
Rotterdam	Rural	–0.22	0.31	0.26	0.22	0.3	0.28	0.39	0.15
Amsterdam	Urban	0.35	0.09+	**0.66**	**<0.001**	–0.27[a]	0.33	–0.09[a]	0.74
Amsterdam	Rural	**0.61**	**0.002**	**0.81**	**<0.001**	0.49[a]	0.06+	**0.89[a]**	**<0.001**
Utrecht	Urban	0.36	0.08+	**0.6**	**0.002**	0.48	0.08+	**0.71**	**0.005**
Utrecht	Rural	**0.59**	**0.002**	**0.64**	**<0.001**	**0.47**	**0.007**	–0.045	0.87
Leidsche Rijn	Urban	0.37	0.08+	0.25	0.24	0.29	0.27	–0.58	0.83
Leidsche Rijn	Rural	**0.56**	**0.004**	**0.78**	**<0.001**	0.38	0.16	0.21	0.46
Schaijk	Urban	**0.73**	**<0.001**	**0.81**	**<0.001**	0.13	0.64	0.47	0.07+
Schaijk	Rural	**0.81**	**<0.001**	**0.5**	**0.031**	**0.73**	**0.001**	–0.09	0.73
Hilversum	Urban	**0.6**	**0.002**	**0.66**	**<0.001**	–0.27	0.32	–0.12	0.67
Hilversum	Rural	0.25	0.24	**0.83**	**<0.001**	–0.17	0.54	**0.68**	**0.005**
The Hague	Urban	0.4	0.054+	0.23	0.28	–0.36	0.17	**–0.5**	**0.05**
The Hague	Rural	**0.43**	**0.036**	**0.73**	**<0.001**	–0.4	0.14	0.23	0.41
Nijmegen	Urban	**0.47**	**0.019**	**0.52**	**0.009**	0.18	0.49	–0.19	0.47
Nijmegen	Rural	**0.69**	**<0.001**	**0.69**	**<0.001**	0.09+	0.75	0.46	0.08+
Leiden	Urban	**0.55**	**0.005**	0.35	0.091+	–0.12	0.64	–0.29	0.26
Leiden	Rural	0.27	0.2	**0.68**	**<0.001**	0.08	0.76	0.46	0.06+

We provide the statistics for the 24 h of data and for the same data, but excluding the night hours. R indicates the coefficient of correlation, and p indicates the p-value of the test. We used a Spearman's correlation rank test or sometimes a Pearson's correlation test (the latter indicated with [a]*). Significant results are indicated in bold and non-significant trend with a +.*

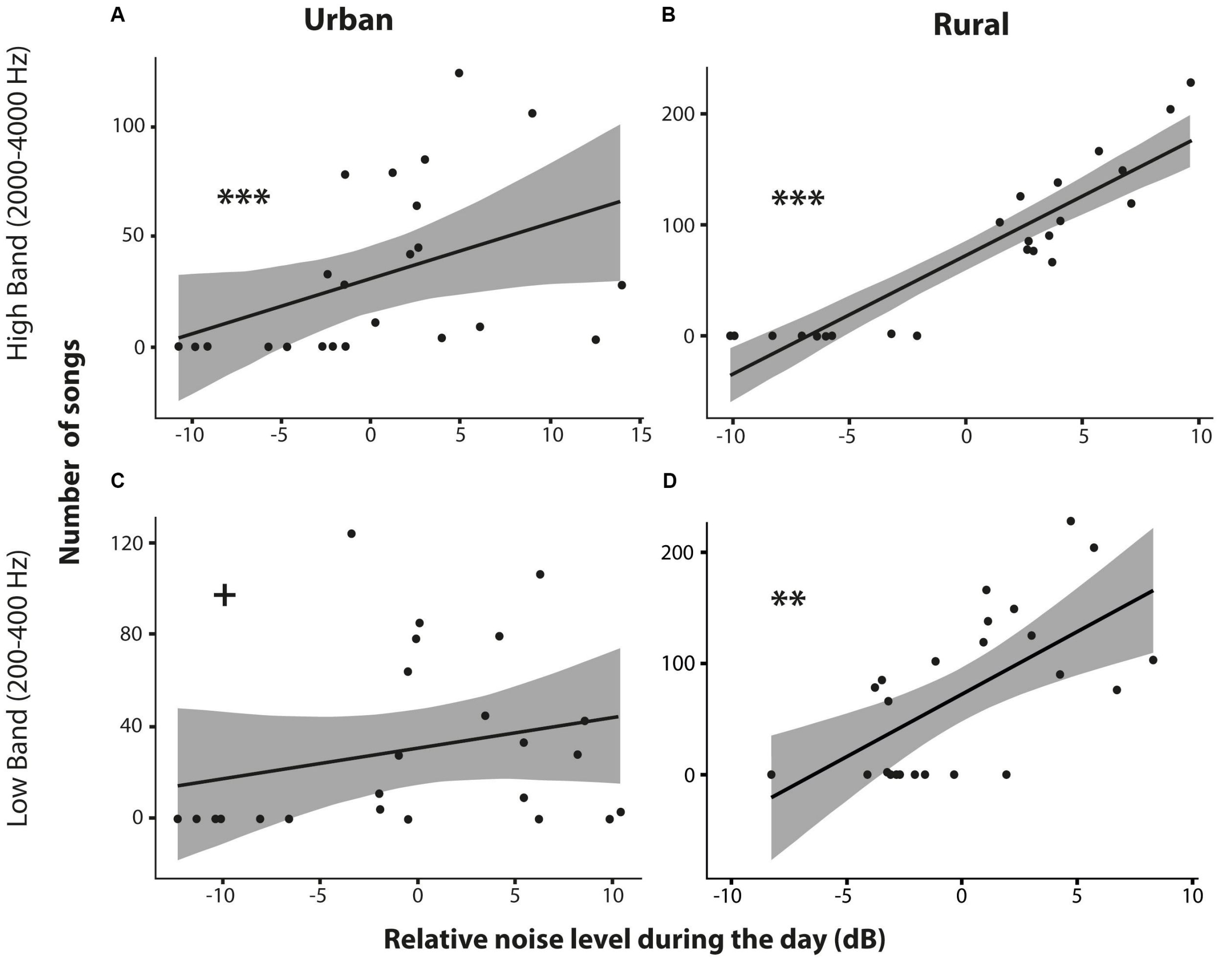

FIGURE 6 | Relationship between the number of songs sung and the relative noise level during the day for the urban and rural pair sites of Amsterdam. Scatterplots for the high band noise (2000–4000 Hz; reflecting bird noise) in the urban **(A)** and rural **(B)** sites, and for the low band noise (200–400 Hz; reflecting traffic noise) in urban **(C)** and rural **(D)** sites (** and *** indicate significant difference at $p < 0.01$ and $p < 0.001$ level and + means a non-significant trend). See text for statistics.

different from rural great tits, but we did find less song in city birds in several hour bins during the rest of the day. This pattern is, as far as we know, the first time this has been shown at this scale, but may indicate that rising early is associated with inserting periods of no or low activity more often during the rest of the day (c.f. de Jong et al., 2016; Raap et al., 2016).

Our data are in line with the growing awareness that the presence of human settlements and infrastructure can alter environmental cues and make urban and rural birds of the same species alter their activity patterns over the day. Cartwright et al. (2014) also conducted a study at high- and low-traffic sites in southern Ontario, Canada. They found that red-winged blackbirds (*Agelaius phoeniceus*), a semi-colonial breeder of marshlands, sang more at dawn and dusk at the rural sites and more during midday at the urban sites. They did not assess daily starting times or dawn chorus duration. It is, nevertheless, interesting that the patterns of singing effort divergence between urban and rural birds are quite different from ours on great tits. We found no difference in amount of singing at the dawn peak, while the divergence during the rest of the day, more singing in rural than urban, was opposite that of red-winged blackbirds. Not only were species and continent different between these studies, but the study of Cartwright et al. (2014) had another limitation that should be reason for caution. Although they recorded the three urban and two rural sites for relatively long periods (6 and 5 weeks, respectively), these periods were not overlapping (May till half-June for urban and end-June till end-July for rural), and a seasonal impact is therefore unknown and confounding with habitat (urban versus rural). As far as we know, there are no other studies that shed light on urban-rural patterns of 24-h activity cycles, but there are quite a few studies that explored the process.

Traffic noise and street lightening are two of the most prominent pollutants that are put forward as causing changes in avian rhythms (Nordt and Klenke, 2013; Lee et al., 2017). American robins (*Turdus migratorius*), for example, initiated their dawn chorus during the night, especially in areas with elevated artificial light levels (Miller, 2006). This pattern has been repeatedly confirmed afterward in several European species across latitude (Da Silva et al., 2014; Dominoni et al., 2014; Da Silva and Kempenaers, 2017). However, a study on European robins (*Erithacus rubecula*) reported nocturnal singing in urban territories with street lights, but attributed a larger proportion of the variation to daytime noise levels than to nighttime light levels (Fuller et al., 2007). For neither of these studies, it is clear whether there was a shift or an extension of activity, as data were not collected for the full day. Another recent study in urban greenspaces (Lee et al., 2017) also reported an impact of both light and noise on dawn chorus timing, with a larger role for artificial light at night, but with an opposite effect from the studies above. Traffic noise appears to be correlated to advancing dawn chorus in tropical bird species as well, where artificial light has apparently less of an effect, probably due to little variation in day length at their latitude (Dorado-Correa et al., 2016; Marín-Gómez and MacGregor-Fors, 2019). Independent of whether artificial light or traffic noise or a third factor is the underlying process, we would like to see more studies that describe the full-day patterns.

Causes and Consequences

A complete description of 24 h cycles is important for hypotheses about a mechanistic understanding of causal relationships in urban activity shifts and for the interpretation of potential consequences. However, experimental approaches will always be critical for proving causal relationships between the manipulated factors, such as light and/or noise level, and the behavioral read-out, for example, dawn chorus timing or singing effort (Arroyo-Solís et al., 2013; Yang and Slabbekoorn, 2014; Da Silva et al., 2017). However, confirmation that one factor plays a role, does not exclude an impact of another. Furthermore, potential consequences depend on many factors, as nighttime light and daytime noise levels may affect the timing and amount of singing, but directly or indirectly also other activities, such as foraging, nest building, scanning for predators, or seeking extra-pair interactions (Raap et al., 2017; Dominoni et al., 2020). We here just address adaptive and non-adaptive explanations for altered activity patterns in vocal behavior.

Adaptive explanations include positive consequences directly or indirectly related to the proven or hypothesized cause. Many studies have hypothesized that singing earlier in response to rising noise levels or at relatively noisy locations may yield a benefit in being more audible when singing at less noisy time periods of the day (Fuller et al., 2007). This was also partly true for great tits in the current study: the earlier dawn chorus yielded more songs in an earlier and quieter hour of the day, while overall urban birds sang less during the rest of the noisy day. However, we did not find a general negative correlation between singing effort and relative noise level. Cartwright et al. (2014) found a different urban–rural divergence pattern but argued similarly that singing less at dawn and dusk and more during the rest of the day was in line with avoiding the most noisy rush hours. Actual proof of any fitness consequences related to a noise-dependent shift does not exist yet, as far as we know.

Waking up by noisy human activities has also been suggested to be adaptive for those species that find food due to human activities (Arroyo-Solís et al., 2013). Two out of six songbird species responded by singing more early on nights of experimental exposure to local recordings of ambient noise in urban streets, which simulated an exceptionally early rise of people. The two species involved were the spotless starling (*Sturnus unicolor*) and the house sparrow (*Passer domesticus*), two typical commensals of human settlements that forage at feeding places. The earlier dawn singing due to artificially high light levels has been proposed to be beneficial for mating opportunities. In blue tits (*Cyanistes caeruleus*), for example, it has been shown that males close to street lights have higher reproductive success and are more attractive to females (Kempenaers et al., 2010), while early singers have been shown to be preferred by females in this species (Poesel et al., 2006). Such strong correlations have not been found for cases where birds sing earlier due to noisy territories, but may also apply, if not outweighed by other negative consequences.

Maladaptive explanations of altered vocal activity patterns are also diverse and may include detrimental consequences related to energy expenditure required for singing in earlier and colder times of day, singing more or with more effort to compensate for challenging signal-to-noise ratios, or singing at the expense of foraging for which there is ample evidence of a trade-off (Ydenberg, 1984; Cuthill and MacDonald, 1990; Grava et al., 2009). Singing earlier or singing less may also make birds more vulnerable to territorial intrusions and may force individuals into physical fight more often, which may bring risk of injury and increased chance of predation. This matches well with a pattern of noise-dependent aggression levels (Slabbekoorn, 2013), for which there is growing evidence from birds in cities (Phillips and Derryberry, 2018) and around airports (Wolfenden et al., 2019). Lower song activity during noisy daytime conditions, as found in our study, also matches with noise-induced rise in vigilance and distraction, which has been shown to reduce foraging efficiency (Quinn et al., 2006; Campbell et al., 2019). Again, actual proof of any negative fitness consequences does also not exist yet. It may also well be that vocal activity shifts in time or effort are not having any adaptive or maladaptive consequences.

CONCLUSION

We have shown conclusively that great tits in urban and rural areas differ in the timing of their singing activity: the dawn chorus starts earlier in the city and after that there is less singing activity in urban streets than in rural woodland. This concerns a confirmation of the early rise in cities as reported for many bird species and attributed sometimes to traffic noise during daytime, to artificial light at night, or both. However, this is the first well-replicated study at habitat level and the first that also scored activity for full 24-h cycles. The latter revealed that an earlier singing start does not mean that urban birds sing more or less, or shorter or longer, during the dawn chorus, but that there is significantly less singing activity afterward during the rest of the day in cities compared to woodland. We currently have no insight into whether this can be related to any mechanistic or functional link between morning and afternoon activities, but this can be an interesting avenue for further study. The pattern shifts also appear to be moderate and may just be a case of non-relevant plasticity, but evidence for or against positive or negative fitness consequences are largely lacking. Nevertheless, we have confirmed here that avian vocal activity shifts are a clear case of how anthropogenic effects on the natural environment influence fundamental aspects of daily life in the animal communities with which we share the urban habitat.

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

Ethical review and approval was not required for this animal study in accordance with the local legislation and institutional requirements.

AUTHOR CONTRIBUTIONS

EB-C and HS designed the project as a part of EB-C's post-doctoral research stay at Leiden University. The fieldwork was carried out by EB-C, ZD, and LV. ZD and LV conducted part of the data processing. CK helped EB-C with the rest of the data processing and data analysis. EB-C contributed to the writing of the manuscript together with HS. All authors contributed to the article and approved the submitted version.

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REFERENCES

Aide, T. M., Corrada-Bravo, C., Campos-Cerqueira, M., Milan, C., Vega, G., and Alvarez, R. (2013). Real-time bioacoustics monitoring and automated species identification. *PeerJ* 1:e103. doi: 10.7717/peerj.103

Arroyo-Solís, A., Castillo, J. M., Figueroa, E., Lopez-Sanchez, J. L., and Slabbekoorn, H. (2013). Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. *J. Avian. Biol.* 44, 288–296. doi: 10.1111/j.1600-048X.2012.05796.x

Ball, G. F. (1999). "Neuroendocrine basis of seasonal changes in vocal behavior among songbirds," in *The Design of Animal Communication*, eds M. Hauser and M. Konishi (Cambridge, MA: MIT Press), 213–253.

Barrueto, M., Ford, A. T., and Clevenger, A. P. (2014). Anthropogenic effects on activity patterns of wildlife at crossing structures. *Ecosphere* 5:27. doi: 10.1890/ES13-00382.1

Berg, K. S., Brumfield, R. T., and Apanius, V. (2006). Phylogenetic and ecological determinants of the neotropical dawn chorus. *Proc. R. Soc. B Biol. Sci.* 273, 999–1005. doi: 10.1098/rspb.2005.3410

Bergen, F., and Abs, M. (1997). Etho-ecological study of the singing activity of the blue tit (*Parus caeruleus*), great tit (*Parus major*) and chaffinch (*Fringilla coelebs*). *J. Ornithol.* 138, 451–467. doi: 10.1007/BF01651380

Bergman, G. (1982). Die Veränderung der Gesangmelodie der Kohlmeise *Parus major* in Finnland und Schweden. *Ornis Fenn.* 57, 97–111.

Blake, J. G. (1992). Temporal variation in point counts of birds in a lowland wet forest in Costa Rica. *Condor* 94, 265–275. doi: 10.2307/1368816

Brown, T. J., and Handford, P. (2003). Why birds sing at dawn: the role of consistent song transmission. *Ibis* 145, 120–129. doi: 10.1046/j.1474-919X.2003.00130.x

Bruni, A., Mennill, D. J., and Foote, J. R. (2014). Dawn chorus start time variation in a temperate bird community: relationships with seasonality, weather, and ambient light. *J. Ornithol.* 155, 877–890. doi: 10.1007/s10336-014-1071-7

Campbell, K. A., Proppe, D. S., Congdon, J. V., Scully, E. N., Miscler, S. K., and Sturdy, C. B. (2019). The effect of anthropogenic noise on feeding behaviour in black-capped chickadees (*Poecile atricapillus*). *Behav. Process.* 158, 53–58. doi: 10.1016/j.beproc.2018.10.015

Caorsi, V., Sprau, P., Zollinger, S. A., and Brumm, H. (2019). Nocturnal resting behaviour in urban great tits and its relation to anthropogenic disturbance and microclimate. *Behav. Ecol. Sociob.* 73:19. doi: 10.1007/s00265-018-2624-1

Cartwright, L. A., Taylor, D. R., Wilson, D. R., and Chow-Fraser, P. (2014). Urban noise affects song structure and daily patterns of song production in red-winged blackbirds (*Agelaius phoeniceus*). *Urban Ecosyst.* 17, 561–572. doi: 10.1007/s11252-013-0318-z

Cuthill, I. C., and MacDonald, W. A. (1990). Experimental manipulation of the dawn and dusk chorus in the blackbird (*Turdus merula*). *Behav. Ecol. Sociobio.* 26, 209–216. doi: 10.1007/BF00172088

Da Silva, A., de Jong, M., van Grunsven, R. H. A., Visser, M. E., Kempenaers, B., and Spoelstra, K. (2017). Experimental illumination of a forest: no effects of lights of different colours on the onset of the dawn chorus in songbirds. *R. Soc. Open Sci.* 4:160638. doi: 10.1098/rsos.160638

Da Silva, A., and Kempenaers, B. (2017). Singing from North to South: latitudinal variation in timing of dawn singing under natural and artificial light conditions. *J. Anim. Ecol.* 86, 1286–1297. doi: 10.1111/1365-2656.12739

Da Silva, A., Samplonius, J. M., Schlicht, E., Valcu, M., and Kempenaers, B. (2014). Artificial night lighting rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. *Behav. Ecol.* 25, 1037–1047. doi: 10.1093/beheco/aru103

Da Silva, A., Valcu, M., and Kempenaers, B. (2015). Light pollution alters the phenology of dawn and dusk singing in common European songbirds. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 370, 20140126. doi: 10.1098/rstb.2014.0126

de Jong, M., Jeninga, L., Ouyang, J. Q., van Oers, K., Spoelstra, K., and Visser, M. E. (2016). Dose-dependent responses of avian daily rhythms to artificial light at night. *Physiol. Behav.* 155, 172–179. doi: 10.1016/j.physbeh.2015.12.012

Dominoni, D., Smit, J. A. H., Visser, M. E., and Halfwerk, W. (2020). Multisensory pollution: artificial light at night and anthropogenic noise have interactive effects on activity patterns of great tits (*Parus major*). *Environ. Pollut.* 256:113314. doi: 10.1016/j.envpol.2019.113314

Dominoni, D. M., Carmona-Wagner, E. O., Hofmann, M., Kranstauber, B., and Partecke, J. (2014). Individual-based measurements of light intensity provide new insights into the effects of artificial light at night on daily rhythms of urban-dwelling songbirds. *J. Anim. Ecol.* 83, 681–692. doi: 10.1111/1365-2656.12150

Dominoni, D. M., Greif, S., Nemeth, E., and Brumm, H. (2016). Airport noise predicts song timing of European birds. *Ecol. Evol.* 6, 6151–6159. doi: 10.1002/ece3.2357

Dominoni, D. M., Helm, B., Lehmann, M., Dowse, H. B., and Partecke, J. (2013). Clocks for the city: circadian differences between forest and city songbirds. *Proc. Biol. Sci.* 280:20130593. doi: 10.1098/rspb.2013.0593

Dorado-Correa, A., Rodriguez-Rocha, M., and Brumm, H. (2016). Anthropogenic noise, but not artificial light levels predicts song behaviour in an equatorial bird. *R. Soc. Open Sci.* 3:160231. doi: 10.1098/rsos.160231

Frey, S., Fisher, J. T., Burton, A. C., and Volpe, J. P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sens. Ecol. Conserv.* 3, 123–132. doi: 10.1002/rse2.60

Fuller, R. A., Warren, P. H., and Gaston, K. J. (2007). Daytime noise predicts nocturnal singing in urban robins. *Biol. Lett.* 3, 368–370. doi: 10.1098/rsbl.2007.0134

Garson, P. J., and Hunter, M. L. (1979). Effects of temperature and time of year on the singing behaviour of wrens (*Troglodytes troglodytes*) and great tits (*Parus major*). *Ibis* 121, 481–487. doi: 10.1111/j.1474-919X.1979.tb06688.x

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., and Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science* 360, 1232–1235. doi: 10.1126/science.aar7121

Gil, D., Honarmand, M., Pascual, J., Perez-Mena, E., and Macias Garcia, C. (2015). Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behav. Ecol.* 26, 435–443. doi: 10.1093/beheco/aru207

Grava, T., Grava, A., and Otter, K. A. (2009). Supplemental feeding and dawn singing in black-capped chickadees. *Condor* 111, 560–564. doi: 10.1525/cond.2009.080061

Halfwerk, W., Bot, S., Buikx, J., Van Der Velde, M., Komdeur, J., Ten Cate, C., et al. (2011). Low songs lose potency in urban noise conditions. *Proc. Natl. Acad. Sci. U.S.A.* 108, 14549–14554. doi: 10.1073/pnas.1109091108

Halfwerk, W., Bot, S., and Slabbekoorn, H. (2012). Male great tit song perch selection in response to noise-dependent female feedback. *Funct. Ecol.* 26, 1339–1347. doi: 10.1111/j.1365-2435.2012.02018.x

Hart, P. J., Hall, R., Ray, W., Beck, A., and Zook, J. (2015). Cicadas impact bird communication in a noisy tropical rainforest. *Behav. Ecol.* 26, 839–842. doi: 10.1093/beheco/arv018

Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous inference in general parametric models. *Biomed. J.* 50, 346–363. doi: 10.1002/bimj.200810425

Hunter, M. L., and Krebs, J. R. (1979). Geographical variation in the song of the great tit (*Parus major*) in relation to ecological factors. *J. Anim. Ecol.* 48, 759–785. doi: 10.2307/4194

Kacelnik, A., and Krebs, J. R. (1983). The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour* 83, 287–309. doi: 10.1163/156853983X00200

Kempenaers, B., Borgström, P., Loës, P., Schlicht, E., and Valcu, M. (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Curr. Biol.* 20, 1735–1739. doi: 10.1016/j.cub.2010.08.028

Krebs, J., Ashcroft, R., and Webber, M. (1978). Song repertoires and territory defence in great tit. *Nature* 271, 539–542. doi: 10.1016/S0003-3472(81)80029-2

Lee, J. G.-H., MacGrgor-Fors, I., and Yeh, P. J. (2017). Sunrise in the city: disentangling drivers of the avian dawn chorus onset in urban greenspaces. *J. Avian Biol.* 48, 955–964. doi: 10.1111/jav.01042

Lehtonen, L. (1983). The changing song patterns of the great tit *Parus major*. *Ornis Fenn.* 60, 16–21.

Lendrum, P. E., Crooks, K. R., and Wittemyer, G. (2017). Changes in circadian activity patterns of a wildlife community post high-intensity energy development. *J. Mammal.* 98, 1265–1271. doi: 10.1093/jmammal/gyx097

Mace, R. (1987). The dawn chorus in the great tit (*Parus major*) is directly related to female fertility. *Nature* 330, 745–746. doi: 10.1038/330745a0

Marchand, P., Garel, M., Bourgoin, G., Dubray, D., Maillard, D., and Loison, A. (2014). Impacts of tourism and hunting on a large herbivore's spatio-temporal behavior in and around a French protected area. *Biol. Conserv.* 177, 1–11. doi: 10.1016/j.biocon.2014.05.022

Marín-Gómez, O. H., and MacGregor-Fors, I. (2019). How early do birds start chirping? Dawn chorus onset and peak times in a neotropical city. *Ardeola* 66, 327–341. doi: 10.13157/arla.66.2.2019.ra5

Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allaine, D., and Swenson, J. E. (2010). Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Can. J. Zool.* 88, 875–883. doi: 10.1139/Z10-053

Miller, M. W. (2006). Apparent effects of light pollution on singing behavior in American robins. *Condor* 108, 130–139. doi: 10.1093/condor/108.1.130

Mockford, E. J., and Marshall, R. C. (2009). Effects of urban noise on song and response behaviour in great tits. *Proc. R. Soc. B* 276, 2979–2985. doi: 10.1098/rspb.2009.0586

Naguib, M., Diehl, J., Van Oers, K., and Snijders, L. (2019). Repeatability of signalling traits in the avian dawn chorus. *Front. Zool.* 16:27. doi: 10.1186/s12983-019-0328-7

Nemeth, E., and Brumm, H. (2010). Birds and anthropogenic noise: are urban songs adaptive? *Am. Nat.* 176, 465–475. doi: 10.1086/656275

Nordt, A., and Klenke, R. (2013). Sleepless in town - Drivers of the temporal shift in dawn song in urban European blackbirds. *PLoS One* 8:e71476. doi: 10.1371/journal.pone.0071476

Nottebohm, F. (1981). A brain for all seasons: cyclical anatomical changes in song-control nuclei of the canary brain. *Science* 214, 1368–1370. doi: 10.1126/science.7313697

Ogurtsov, S., Zheltukhin, A. S., and Kotlov, I. (2018). Daily activity patterns of large and medium-sized mammals based on camera traps data in the Central Forest Nature Reserve, Valdai Upland, Russia. *Nat. Conserv. Res.* 3, 68–88. doi: 10.24189/ncr.2018.031

Pérez-Granados, C., Osiejuk, T. S., and López-Iborra, G. M. (2018). Dawn chorus interpretation differs when using songs or calls: the Dupont's Lark *Chersophilus duponti* case. *PeerJ* 6:e5241. doi: 10.7717/peerj.5241

Phillips, J. N., and Derryberry, E. P. (2018). Urban sparrows respond to a sexually selected trait with increased aggression in noise. *Sci. Rep.* 8:7505. doi: 10.1038/s41598-018-25834-6

Poesel, A., Kunc, H. P., Foerster, K., Johnsen, A., and Kempenaers, B. (2006). Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, *Cyanistes* (formerly *Parus*) *caeruleus*. *Anim. Behav.* 72, 531–538. doi: 10.1016/j.anbehav.2005.10.022

Pohl, N. U., Slabbekoorn, H., Klump, G. M., and Langemann, U. (2009). Effects of signal features and environmental noise on signal detection in the great tit, Parus major. *Anim. Behav.* 78, 1293–1300. doi: 10.1016/j.anbehav.2009.09.005

Quinn, J. L., Whittingham, M. J., Butler, S. J., and Cresswell, W. (2006). Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. *J. Avian Biol.* 37, 601–608. doi: 10.1111/j.2006.0908-8857.03781.x

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. Vienna: R Core Team.

Raap, T., Pinxten, R., Casasole, G., Dehnhard, N., and Eens, M. (2017). Ambient anthropogenic noise but not light is associated with the ecophysiology of free-living songbird nestlings. *Sci. Rep.* 7:2754. doi: 10.1038/s41598-017-02940-5

Raap, T., Pinxten, R., and Eens, M. (2016). Artificial light at night disrupts sleep in female great tits (*Parus major*) during the nestling period, and is followed by a sleep rebound. *Environ. Pollut.* 215, 125–134. doi: 10.1016/j.envpol.2016.04.100

Senar, J. C., Garamszegi, L. Z., Tilgar, V., Biard, C., Moreno-Rueda, G., Salmón, P., et al. (2017). Urban great tits (*Parus major*) show higher distress calling and pecking rates than rural birds across Europe. *Front. Ecol. Evol.* 5:163. doi: 10.3389/fevo.2017.00163

Sierro, J., Schloesing, E., Pavon, I., and Gil, D. (2017). European blackbirds exposed to aircraft noise advance their chorus, modify their song and spend more time singing. *Front. Ecol. Evol.* 5:68. doi: 10.3389/fevo.2017.00068

Slabbekoorn, H. (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* 85, 1089–1099. doi: 10.1016/j.anbehav.2013.01.021

Slabbekoorn, H., and den Boer-Visser, A. (2006). Cities change the songs of birds. *Curr. Biol.* 16, 2326–2331. doi: 10.1016/j.cub.2006.10.008

Slabbekoorn, H., and Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature* 424:267. doi: 10.1038/424267a

Slabbekoorn, H., and Ripmeester, E. A. P. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Mol. Ecol.* 17, 72–83. doi: 10.1111/j.1365-294X.2007.03487.x

Slagsvold, T., Dale, S., and Saetre, G. P. (1994). Dawn singing in the great tit (*Parus major*): mate attraction, mate guarding or territorial defense. *Behaviour* 131, 115–138. doi: 10.1163/156853994X00244

Stanley, C. Q., Walter, M. H., Venkatraman, M. X., and Wilkinson, G. S. (2016). Insect noise avoidance in the dawn chorus of Neotropical birds. *Anim. Behav.* 112, 255–265. doi: 10.1016/j.anbehav.2015.12.003

Swaddle, J. P., Francis, C. D., Barber, J. R., Cooper, C. B., Kyba, C. C. M., Dominoni, D. M., et al. (2015). A framework to assess evolutionary responses to anthropogenic light and sound. *Trends Ecol. Evol.* 30, 550–560. doi: 10.1016/j.tree.2015.06.009

Ulgezen, Z. N., Kapyla, T., Meerlo, P., Spoelstra, K., Visser, M. E., and Dominoni, D. M. (2019). Preference and costs of sleeping under light at night in forest and urban great tits. *Proc. R. Soc. B* 286, 20190872. doi: 10.1098/rspb.2019.0872

Wolfenden, A. D., Slabbekoorn, H., Kluk, K., and de Kort, S. R. (2019). Aircraft sound exposure leads to song frequency decline and elevated aggression in wild chiffchaffs. *J. Anim. Ecol.* 88, 1720–1731. doi: 10.1111/1365-2656.13059

Yang, X. J., and Slabbekoorn, H. (2014). Timing vocal behavior: lack of temporal overlap avoidance to fluctuating noise levels in singing Eurasian wrens. *Behav. Process.* 108, 131–137. doi: 10.1016/j.beproc.2014.10.002

Ydenberg, R. C. (1984). The conflict between feeding and territorial defence in the Great Tit. *Behav. Ecol. Sociobiol.* 15, 103–108. doi: 10.1007/BF00299376

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Temporally Separated Data Sets Reveal Similar Traits of Birds Persisting in a United States Megacity

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We present an analysis of life history and behavioral traits associated with urbanization for 52 breeding bird species on 173 survey blocks in the Los Angeles area of southern California, United States, across two time periods, 1995–1999 and 2012–2016. We used observational data from two community science efforts and an estimate of urban land cover in each block to develop an index of urban association, and then modeled the relationship between species occurrence and eight traits likely associated with urban tolerance. We found two traits to be significantly associated with urbanization in both eras: Structure-nesting (i.e., the tendency to build nests on human-built structures) was positively associated, and cavity-nesting (i.e., the tendency to build nests in natural tree cavities) was negatively associated. Our analysis provides a template for mining historical community science data, and for "retrofitting" contemporary data to gain insights into ecological trends over time, and illustrates the persistence of ecological traits of species associated with urban areas even as the makeup of these species communities may change.

Keywords: community science, citizen science, California, eBird, breeding bird atlas, life history traits, urban tolerance

INTRODUCTION

Understanding species' tolerance to urbanization will be key to conserving biotic diversity as global population increases and as more people move to cities (Vitousek et al., 1997; Marzluff, 2005). Various external factors, including mechanical noise, anthropogenic light, windows, and outdoor cats represent direct, urban-associated influences on bird distributions (reviewed by Marzluff, 2016). The process by which species invade and exploit novel environments has been referred to as "filtering" (Clergeau et al., 2001), and may be applied to those bird communities in or near urban areas, with certain species passing through the urban filter successfully or invading following urbanization, and others failing to do so (Lowry et al., 2013; Wingfield et al., 2015). Johnston (2001) recognized a gradient of tolerance from urban avoidance to synanthropy, or a dependence on the built environment, and this vocabulary has been expanded by numerous authors (e.g., "specialist" vs. "mutualist" species, from MacGregor-Fors and Ortega-Alvarez, 2011) to describe the affiliation between certain species and urban areas.

While urbanization tends to homogenize formerly complex ecological systems (McKinney, 2006; Devictor et al., 2007), certain specialist taxa may exploit urban sites preferentially, or may assemble into novel communities there (Møller et al., 2015), particularly where urban habitats are more structurally complex than those replaced, such as grassland or low scrub (e.g., Emlen, 1974; Gonzalez-Garcia et al., 2014). Certain types of food/prey and nesting sites may be superabundant in urban areas, owing to the presence of lush, landscaped vegetation, anthropogenic water and supplemental feeding (Chace and Walsh, 2006), though this availability may be offset by novel hazards such as feral cats (Loss et al., 2013). Thus, not all species that thrive in urban areas are drawn to hardscape or modified vegetation; some may simply maintain populations in habitat fragments within an otherwise urbanized landscape, for example marsh-dwelling birds occurring at small urban wetlands, along flood-control channels.

Efforts to identify traits that allow species (or individuals of the same species) to tolerate and even thrive with urbanization date to the early 1960s; more recently, the term "urban bird syndrome" has been coined to capture behavioral, physical, reproductive, and ecological traits (see Møller, 2014; Samia et al., 2015 for meta-analyses and summaries of prior findings). Urban birds tend to display behavioral boldness and "innovation propensity," which compels individuals to explore new habitats and become established in these areas (Atwell et al., 2012; Blumstein, 2014; see review by Sol et al., 2017). They have shorter flight initiation distances (FID) and exhibit heightened predator avoidance (Blumstein, 2006; Møller, 2010), heightened territoriality and aggression (Evans et al., 2010), and reduced vocalizations (Estes and Mannan, 2003). They also tend to have a broader elevational tolerance (Bonier et al., 2007) and a larger geographical range (Møller, 2009). Morphological variables have also been found to be associated with urbanization in birds, including body size (small size for raptors; Chace and Walsh, 2006), and wingspan (large wingspan for passerines; Croci et al., 2008). It is important to note that these studies include those that compared traits across multiple species, as well as those that investigated traits of individuals within the same species.

Diet studies have consistently found positive associations between urbanization and granivory, and negative associations between urbanization and insectivory, including for ground-foraging insectivores (Kark et al., 2007; Croci et al., 2008; Evans et al., 2011; reviewed by Chace and Walsh, 2006). Habitat preference studies have found that urban passerines are disproportionately represented by forest species (Croci et al., 2008), and by species exhibiting a wide habitat breadth (Sol et al., 2014). Urban birds also tend to be non-migratory both globally (Sol et al., 2014) and regionally in Europe (Croci et al., 2008) and Israel (Kark et al., 2007).

Many breeding behaviors have also been associated with urbanization, and studies examining nesting phenology have found earlier nest initiation both for urban raptors (Boal and Mannan, 1999; Kettel et al., 2018), and for species that visit (urban) feeders (O'Leary and Jones, 2006). Several authors have noted that urban areas would favor species that nest on human-made structures tend (reviewed by Chace and Walsh, 2006), and would disadvantage those that use natural cavities (Blewett and Marzluff, 2005) as well as ground-nesting species (Evans et al., 2011; Sol et al., 2014). Comparisons of nest productivity, clutch size, nest site preference and food-provisioning (to young) among urban bird populations have yielded contradictory results, as noted by Chace and Walsh, (2006; see also Lowry et al., 2013; Marzluff et al., 2015). Likewise, there appears to be little difference in the cognitive abilities of urban vs. rural populations of the same species, as measured by problem-solving ability and relative brain size (e.g., Carrete and Tella, 2011; Sol et al., 2014).

But do these patterns persist through time, in that the same traits that connote success in urban areas do so year after year? Marzluff et al. (2001) recommended that tolerance to urbanization be re-assessed for species over time, because patterns of human activity are constantly changing, with cities adopting new architectural styles and landscaping palettes. A species' basic behavior also may change as populations become more tolerant to human disturbance; for example, they may become habituated to elevated noise and city lights (e.g., Slabbekoorn and den Boer-Visser, 2006; Francis et al., 2009). Conversely, for the most sensitive species, even slight increases in human disturbance may have lasting negative consequences (e.g., from recreational activity within natural open space areas, Pauli et al., 2016), leading to loss of biodiversity over time. Thus, behavioral plasticity, as well as tolerance, may also connote success in urban areas, where birds that readily alter their behaviors would thrive in cities, while those that cannot either decline and vanish, or they never colonize (West-Eberhard, 1989; Sol et al., 2013; Jokimäki et al., 2017). While studies of bird assemblages across gradients of urbanization ("space for time") date to the 1970s (Emlen, 1974; Beissinger and Osborne, 1982; Blair, 1996), those that investigate the same community over time are much less common (but see Aldrich and Coffin, 1980; Shultz et al., 2012), and we are not aware of any that explicitly investigate ecological traits associated with urbanization across two temporal eras.

The Los Angeles metropolitan area of southern California, United States (which includes the city of Los Angeles), is an ideal place to study urban tolerance and persistence in bird species, due to its long history of ornithological investigation (e.g., Grinnell, 1898; Swarth, 1900), its high human population, the large areas of open space present around its borders and even within the urban core, and its large and active birding and citizen-scientist community (Higgins et al., 2019; Li et al., 2019). Its diverse avifauna is also in constant flux in terms of species abundance and distribution (Allen et al., 2016; Garrett, 2018); some local species have long been present and common in Los Angeles' urban environment, such as House Finches (*Haemorhous mexicanus*), while others, such as Dark-eyed Juncos (*Junco hyemalis*), appear to be in a more recent process of shifting from wildland-favoring and somewhat migratory, to ubiquitous year-round residents (Yeh, 2004).

We developed two separate databases separated by nearly 20 years, "retrofitting" modern eBird data[1] to an older dataset from the breeding bird atlas effort in the 1990s (Allen et al., 2016) to understand: (a) which ecological, behavioral and morphological traits of nesting birds are associated with urban landscapes, and (b) whether this has changed in the past 15–20 years. We calculated an "urban index" for each species based on its detections within each of 173 survey blocks, correlated with urban cover data. This index served as a measure of association with urbanization, and we used this value as a response variable in multiple models incorporating eight life history and behavioral traits, body mass, nest height (lowest), ground foraging, migratory status, natural cavity nesting, artificial structure nesting, habitat breadth, and diet breadth. We fitted this model for both the early era and late era datasets, and examined whether the same traits were associated with our urban index during each era.

By examining a range of traits that may account for shifts in range across the region, we aimed to gain insights into possible mechanisms behind species' increases and decreases in urban areas, and potentially resolve some of the previously contradictory findings about species traits associated with urban areas. Our findings may have conservation implications, because the presence of typically urban-avoiding species can be seen as an indication of ecosystem health, while conversely, the spread and prevalence of urban-tolerant species may indicate an ecosystem that has been disrupted, or one that has changed from its former, more natural state. By using two different datasets, separated by up to 20 years, we test the durability of these findings to explain patterns of urban association in birds.

MATERIALS AND METHODS

Study Area

We consider the "Los Angeles area" to be the entire southern half of the ca. 10,000 km^2 expanse of Los Angeles County, which includes all or portions of more than 80 incorporated cities. The study area includes all coastal-draining land in the county below ca. 1,000 m above sea level, from the Santa Monica Mountains and San Fernando Valley east through the San Gabriel Valley to the San Bernardino County line, south to the Pacific Ocean, including the Puente Hills and Palos Verdes Peninsula, while excluding offshore islands (**Figure 1**). The native habitats of the Los Angeles area, now largely limited to its perimeter (but penetrating the central urban core via the Santa Monica Mountains), include a diverse mix of evergreen chaparral (dominated by large shrub species in the Anacardiaceae, Rosaceae, and Rhamnaceae families), low, summer-deciduous scrub (including coastal sage scrub, featuring sages *Salvia* spp.), patches of evergreen woodland (dominated by coast live oak *Quercus agrifolia*), plus numerous microhabitats such as riparian woodland and scrub, alluvial fan scrub, and both seasonal and permanent wetlands (e.g., Schoenherr, 1992; Stein et al., 2007). Historically, the floor of the Los Angeles Basin was dominated by low scrub and prairie-like grassland, now essentially replaced by residential and commercial development.

We excluded the Santa Clara River valley/Santa Clarita area north of the study area, because it is separated from the main Los Angeles Basin by a high pass (Newhall Pass) and features a slightly different avifauna typical of more interior locations in the state. While the study area includes many microclimates (e.g., the coastal areas are cooler during the summer than the interior areas), no major natural impediments to bird dispersal exist.

Urban Cover

Because urban areas may be defined at multiple scales, there is neither global consensus on what constitutes "urban habitat," nor on how best to describe habitats modified by humans yet still retaining important natural elements (Croci et al., 2008; MacGregor-Fors, 2010; Evans et al., 2011; Beninde et al., 2015; but see White et al., 2005; Li et al., 2019). As a measurement of the degree of urbanization in our study area, we calculated urban cover using the "Urban/Built-Up" category in the statewide vegetation mapping dataset "CALVEG," which was created between 2002 and 2003 (CALVEG, 2009; 1 ha mapping units). CALVEG was found to be the most popular California vegetation layer in a recent online survey (Center for Geographical Studies, 2015), and is frequently used in species distribution studies at the scale of ours (e.g., Santos et al., 2017; City of Los Angeles, 2018). This catch-all Urban/Built-Up coverage includes human-made structures such as buildings and roads, but also manicured parks, golf courses and cemeteries, which, in the Los Angeles area, tend to lack natural, native vegetation (as of 2003). Our urban cover designation includes the habitat now commonly referred to as "urban forest" (Wood and Esaian, 2020), as distinct from natural open space, which may include native forest types, as well as many other natural habitat types. We overlaid the survey block boundaries onto the urban/built-up coverage using QGIS (QGIS Development Team,, 2016), and calculated the amount of urban cover in each of the 173 survey blocks (for a description of survey blocks see Breeding Bird Data).

We used the same urban cover values when modeling both the early and late era datasets (our CALVEG coverage was developed in the years between the two eras), because separate land use data at a suitable scale do not exist for each era. We recognize that both housing density increases and localized development continues to occur across the study area (ca. 3% increase in the county's population between 2000 and 2010; Los Angeles Almanac,, 2019) and that absolute tree cover increased dramatically over the past century as the urban forest replaced a landscape that had been dominated by arid scrub and grassland (Gillespie et al., 2011). However, relative urbanization within the study area have remained constant across our survey blocks, in that the most highly urbanized blocks were highly urban in both the early and late era used here, and the least urbanized blocks in the 1990s are still the least urbanized today, such as those in the Santa Monica Mountains (see maps in Lee et al., 2017).

Species Selection

Of the 228 bird species in the Los Angeles County Breeding Bird Atlas, we eliminated 176 species of these due to various

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[1] www.ebird.org

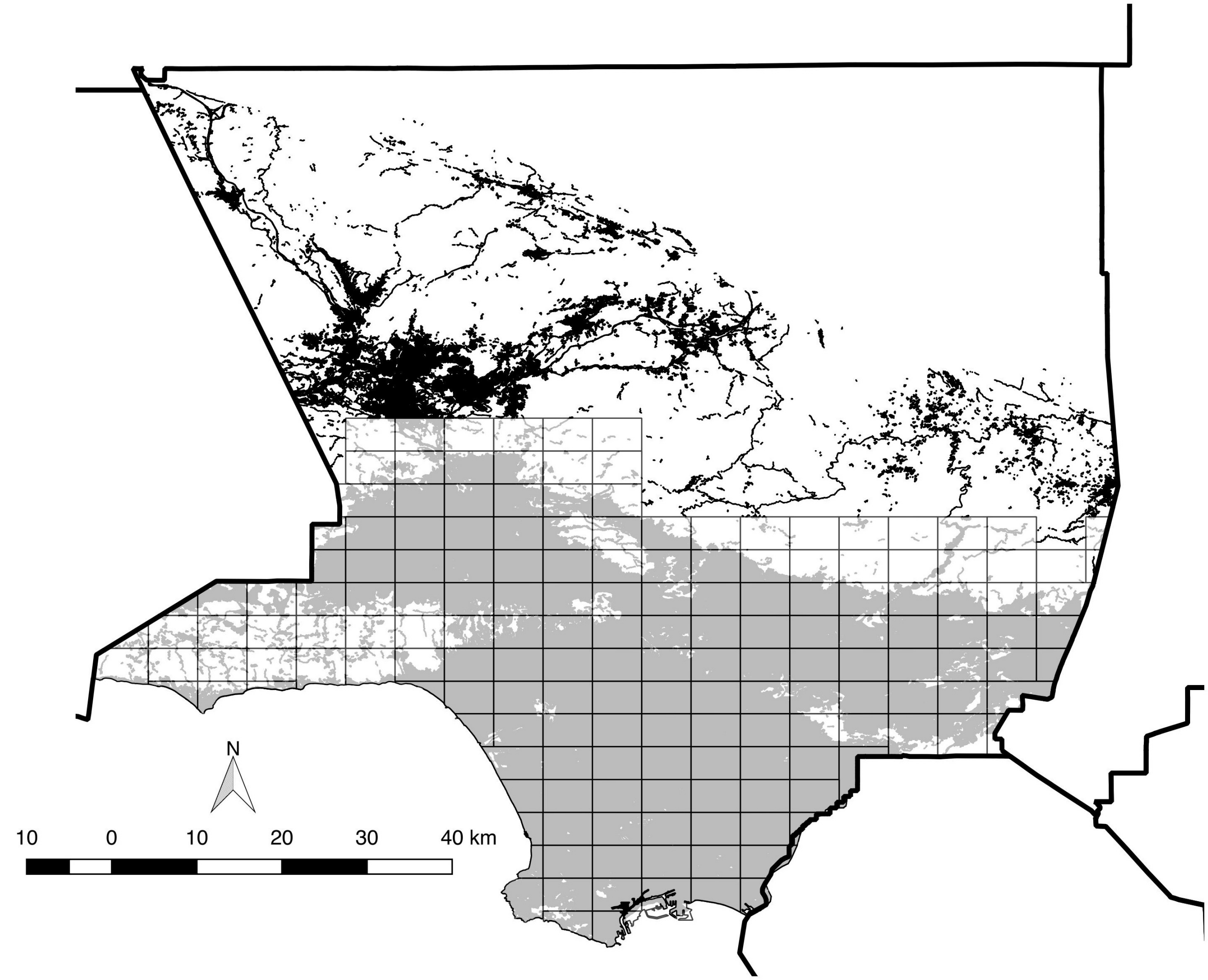

FIGURE 1 | Map of the 173 survey blocks across the study area. Thick solid lines indicate county boundaries (County boundaries downloaded from https://data.ca.gov). Gray-shaded areas indicate modern distribution of "urban" vegetation cover (as defined by CALVEG, 2009) within the study area, and white areas are undeveloped open space comprised of various habitat types. The black shading to the north denotes urban vegetation cover outside the study area. Note that non-urban/wildland habitats are clustered toward the north and west, but also occur near the center of the study area.

factors that would interfere with an analysis of urban association, including very low regional population size, specific microhabitat requirements (which may not be present throughout the study area), and tendency to wander during the breeding season. We first excluded species that occur only in montane/desert areas outside the Los Angeles area, and marine species found along the immediate coast or on offshore islands. We then excluded species due to regional rarity (i.e., those detected on <30 survey blocks of the study area during the breeding season in both the early and late eras), since we were interested in birds that could potentially occur anywhere in the study area, and that were not in low numbers due to some other factor. We then eliminated those associated with specific and localized habitats, such as wetlands, riparian, specific types of scrub, and those known to be grassland-obligate species, since these habitats were found narrowly and patchily in the study area, and likely contribute more to the distribution of species than degree of urbanization. We further eliminated nocturnal species, as well as aerial foragers such as swallows (Hirundinidae) and those species that travel widely, often across multiple survey blocks, during daily foraging activity (e.g., Psittacidae), to avoid counting the same individual birds in multiple blocks and assuming they were breeding in these blocks. Finally, we eliminated species that tend to have such protracted migratory periods that it is difficult to tell when they are actually on breeding territories or simply moving through, such as Black-headed Grosbeaks (*Pheucticus melanocephalus*), which frequently wander through the region for much of the late spring/summer (see Unitt, 2004).

Our final list of 52 species thus includes those that were: (a) widespread enough to be found (or expected) across the study area, (b) likely nesting where they are detected in spring/early summer, and c) habitat generalists, occurring in woodland and shrubby vegetation that represents the dominant habitat across the Los Angeles area, and which is simulated by ornamental plantings such as hedges and street trees. We included several introduced taxa that we knew to be tied to urbanized/modified habitats, such as Scaly-breasted Munia (*Lonchura punctata*). Our final focal species list thus represents a mix of resident and migratory status, size classes (e.g., raptors to hummingbirds), and a diversity of morphological and ecological attributes, with each species having the potential to occur as breeding species in all regions of the study area, and whose presence on a survey block during the breeding season would strongly suggest local nesting on that block.

Breeding Bird Data

BBA (Early Era Dataset)

From 1995 to 1999, the Los Angeles County Breeding Bird Atlas was organized around 414 blocks based on USGS topo quads (each roughly 5.8 km E–W × 4.6 km N–S, or 2,668 hectares; some blocks were larger or smaller along county lines). Each atlas volunteer was assigned one or more blocks and given detailed instructions on how to confirm nesting for as many species as possible within that block, over the span of 5 years. Species were assigned three levels of breeding status for each block (i.e., "confirmed," "probable," or "possible" breeding) based on standardized breeding indicators used during the atlas effort (e.g., singing male represented "possible" breeding, carrying nesting material and feeding young represented "confirmed" breeding, etc.). All data were pooled into an overall "highest breeding status" value, by block, and no specific effort data were collected during the atlas project (i.e., how much observational time was spent within each block). In all, 22,840 records were amassed for 228 species (not all of them confirmed as breeding) by 98 observers searching their blocks. An additional 5,320 "casual observations" by 218 observers were submitted to the atlas project during the atlas period, for a total of 28,935 breeding records analyzed and vetted by staff of the Natural History Museum of Los Angeles County (Allen et al., 2016). We analyzed only the 173 atlas blocks that fell within our coastal lowland study area (see section "Study Area").

EBird (Late Era Dataset)

Data from eBird[2] are collected in a completely different way than the BBA data, with sightings submitted opportunistically by birders from either a specific, georeferenced location, or from somewhere within a larger "hotspot" (typically a park or a trail). EBird data prior to 2,000 are relatively sparse compared to more recent years (hence our incorporation of breeding bird atlas data), and the platform continues to gain in global popularity (as of December 2019, eBird "checklists" – observations of one or more species by a registered eBird user for a particular location, date and time period – were being submitted at the rate of ca. 50,000 per year for Los Angeles County, one of the most actively birded regions of the world). After obtaining all Los Angeles County eBird records for 2012–2016 (1.36 million records), We used the software R (version 3.4.1., R Foundation for Statistical Computing, Wien, Austria) to create a database of sightings that fit our criteria for analysis. Some "coarsening" was necessary to directly compare the breeding status of species from the BBA to that derived from eBird data, as BBA data were reported at the level of atlas block, while eBird data is reported by point data. We assigned each eBird record to a particular atlas block using a spatial join function in QGIS (QGIS Development Team,, 2016).

To further refine the eBird data, records of each focal species were filtered by "safe date," a range of dates for which the presence of that species within a set of dates would be indicative of at least "possible" breeding in the County, as determined during the atlas effort. In certain cases, we used the reported dates of local breeding in lieu of safe dates (e.g., for "breeds late March to early July," we used March 15 to July 15) if they were not provided by Allen and Garrett (1995) for the atlas. Records outside these dates were discarded. Because observations of breeding behavior are not frequently reported in eBird checklists, we could rarely distinguish between "probable" and "confirmed" breeding. Therefore, we considered each species "probable/confirmed" for a given survey block if more than two individuals were observed at a single location (i.e., eBird Hotspot or personal location) during the safe (or designated breeding) dates for any year during the 2012–2016 period. We assigned species as being a "possible" breeder in the block if just one individual was detected with the safe dates, and noted a species as "not breeding" if it was not recorded at all within safe dates.

Because we had no observer effort associated with the BBA data, we did not calculate observer effort for the late era (eBird) data, but worked under the assumption that the most-visited sites in the late 1990s were the same (or were in the same survey blocks) as those from 2012–2016. Likewise, we maintained a conservative approach in data analyses and did not attempt to calculate species abundance within blocks, nor number of years when observed, but simply counted a bird as achieving the highest breeding category during a particular span of years (i.e., replicating what was done for the BBA project). As reviewed by Horns et al. (2018) eBird data, even while opportunistically collected, produces similar results to other forms of observational data collection across large geographical scales, so we felt comfortable comparing the two datasets (BBA and eBird).

Breeding Level and Urban Index

We entered three "breeding levels" for each species, for each survey block, during each era (0 = no record, 1 = possible breeding or 2 = probable/confirmed breeding). We then calculated an "urban index" for each species during each era, which was the correlation coefficient between that species' breeding level within each block (0–2) and the percent urban cover value within that block, using a Spearman's rank test with the rcorr function in R using the Hmisc package (Harrell, 2004). A positive urban index would indicate a positive association between a species and urban cover, while a negative urban index would indicate a negative association with urban cover; an urban index near zero would indicate no association with urban cover. The urban index served as our response variable,

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[2] www.eBird.org

and formed the basis for our trait analysis, below (see also **Supplementary Table S1**).

Because the survey blocks used are arranged in a grid, and urban development in the Los Angeles area includes large, continuous areas of urbanization (as well as large blocks of open space), urban cover was necessarily autocorrelated (Moran's I observed: 0.019, expected: −0.006, $SD = 0.009$, $P = 0.010$). We sought to reduce any error introduced via spatial autocorrelation by using a single urban index value for each species, which was not spatially explicit, but reflected the association between bird distribution and urban cover.

We first tested for a phylogenetic signal in the urban index values for both the early/BBA values and the late/eBird values, using models that employed three different modes of evolution: Brownian motion, Pagel's lambda, Ornstein–Uhlenbeck, as well as a non-phylogenetic model (see Münkemüller et al., 2012). We used the ape (Paradis et al., 2004), geiger (Pennell et al., 2014), and picante (Kembel et al., 2010) packages in R, and used the phylosignal function to analyze the focal species' urban index relative to their corresponding positions on the phylogenetic tree described above. We first tested a Brownian motion, or random-walk model, using a Blomberg's K test (Blomberg et al., 2003), which compares the variance of phylogenetic independent contrasts to what we would expect under a Brownian motion (BM) model. Here, $K = 1$ means that relatives resemble one another as much as we should expect under BM; $K < 1$ means that there is less "phylogenetic signal" than expected under BM, while $K > 1$ means that there is more. We then analyzed the urban index and tree data using Pagel's lambda (Pagel, 1999). Here, if our estimated lambda = 0, then the traits are inferred to have no phylogenetic signal. Lambda = 1 corresponds to a Brownian motion model; 0 < lambda < 1 is intermediate. Finally, we used a model which employed the Ornstein–Uhlenbeck (OU) mode of evolution which incorporates stabilizing selection wherein the trait is drawn toward a fitness optimum, or long-term mean, rather than being completely random and directionless (Martins, 1994). To test for no phylogenetic signal, we also used a "no-signal" generalized least squares model where lambda was set to 0.

Trait Analysis

We identified eight life history and behavioral traits likely associated with urban tolerance based on those identified in previous studies (e.g., Møller, 2014; Samia et al., 2015): body mass, nest height (lowest), ground foraging, migratory status, natural cavity nesting, artificial structure nesting, habitat breadth, and diet breadth (**Table 1**). We were limited in which variables we could use for subsequent modeling by data gaps (e.g., flight initiation distance has been calculated for fewer than half the focal species; D.T. Blumstein, unpubl. data). To account for phylogenetic relatedness among species in our analyses, we used an avian phylogeny from Bird Tree (Jetz et al., 2012, 2014). With our list of 53 species, we used the phylogeny subset tool (in Bird Tree) to create 1,000 trees built with a Hackett et al. (2008) backbone. For use in subsequent analyses, we created a majority-rule consensus tree, collapsing nodes that did not show up in at least 50% of the 1,000 trees.

TABLE 1 | Functional traits considered for this analysis.

Trait	Description	Source
Adult body mass	Total weight (grams; of male if different)	Dunning, 2007
Lowest nest height	Meters; lowest average nest height	Ehrlich et al., 1988; BNA
Forage ground only (during breeding season)	Categorical (2; 0/1); forages exclusively or mainly on the ground	Wilman et al., 2014
Migratory status	Categorical (2; 0/1); non-migratory, partially/fully migratory	eBird
Cavity nest	Categorical (2; 0/1); frequently uses tree cavities for nesting.	Allen et al., 2016
Structure nest	Categorical (2; 0/1); frequently uses human-made structures for nesting (excluding bird boxes)	Allen et al., 2016
Habitat breadth	Level (3; 1–3)	Garrett and Dunn, 1981
Diet breadth	Level (6; 1–6)	Sekerciglou, unpubl. data

BNA, Birds of North America (various authors, https://birdsna.org/).

We then tested the association between these traits and each species' affiliation for urban cover using the urban index as the dependent variable (using both the "early" and "late" values in separate tests), and the eight traits as independent variables. In separate tests (early and late) we ran three phylogenetic generalized least squares (PGLS) tests and one non-phylogenetic GLS tests using each, and compared AIC values of each to select the model that best explained variation in the data.

We used the gls function in the *nlme* package in R (Pinheiro et al., 2019), and incorporated a Brownian motion mode of evolution using the corBrownian function in the phytools package in R (Revell, 2012), along with our phylogenetic tree data. We conducted a second PGLS test using the Ornstein–Uhlenbeck (OU) mode of evolution using the corMartins function in the *sde* package in R (Iacus, 2016). We conducted a third PGLS test using Pagel's lambda test with the corPagel function also in the *sde* package. We fitted a non-phylogenetic least squares model to compare with the PGLS tests. For all analyses, best fit parameters of the phylogenetic model were estimated with maximum likelihood. Lastly, we checked residuals for normality using QQ tests, and selected the analysis with the lowest AIC values as the best model.

RESULTS

Urban Index

Nearly all focal species (48 of 52 species) showed an increase (i.e., toward positive) in urban index over time (**Supplementary Table S1**), and while we cannot directly compare urban indices between the two eras due to the different methodologies used in data collection, some of these species shifted from a negative or neutral urban index to a positive one, suggesting they may now be *preferring* urban habitats – or, at least, natural habitats near urban areas – over blocks with a greater percentage of natural vegetation. These "shifters" include representatives from diverse families, including Cooper's Hawks (*Accipiter cooperii*) (−0.34 to 0.15), Allen's Hummingbirds (*Selasphorus sasin*) (0.10 to 0.24), and Hooded Orioles (*Icterus cucullatus*) (−0.15 to 0.15). At the other end of the spectrum, those with the largest negative residual values include California Quail (*Callipepla californica*), Wrentits (*Chamaea fasciata*) and Spotted Towhees (*Pipilo maculatus*). By contrast, very few species shifted from positive (i.e., more urban-associated) to negative (**Supplementary Table S1**). We plot species' representation on survey blocks (**Figure 2A**) as well as the urban indices for each species (**Figure 2B**), showing that both values are highly correlated across eras ($r_p = 0.80$, $P < 0.001$ for number of blocks where suspected/confirmed breeding; $r_p = 0.90$, $P < 0.001$ for urban index).

We found no indication of a phylogenetic signal in the urban index value using three phylogenetic models (Brownian motion, O–U, and Pagel's lambda), with the non-phylogenetic model returning the lowest AIC value (**Table 2**).

Trait Analysis

We found that two traits (cavity-nesting and structure-nesting) were significantly associated ($p < 0.05$) with urban index values using both the early and late eras in most models examined. We found migratory status was significantly associated with urbanization in the early era dataset (but not in the late era dataset). Cavity-nesting and migratory status were negatively associated with the urban index (that is, cavity-nesting and migratory birds were more associated with natural habitat), while structure-nesting was positively associated with the urban index. While the AIC score of the non-phylogenetically informed GLS was not sufficiently different from the OU and Pagel's lambda models (**Table 3**), these models had nearly identical associations with urban index in both the early and late era datasets. We summarize the results of the best model (non-phylogenetically informed GLS) in **Table 4**.

Non-significant negative associations were detected in several models (including the best/non-phylogenetically informed GLS model) for body mass, ground-foraging, migratory status and habitat breadth, and non-significant positive associations with nest height and diet breadth. While they did not rise to the level of significance (i.e., $P > 0.05$), they were consistent in their direction across temporal eras.

DISCUSSION

Our study is one of very few to analyze the persistence of avian traits using both historical and current community-science data, and adds to an ample literature on why some birds thrive in urban areas and others avoid them. Our results suggest that nest site choice and migratory status may confer either an

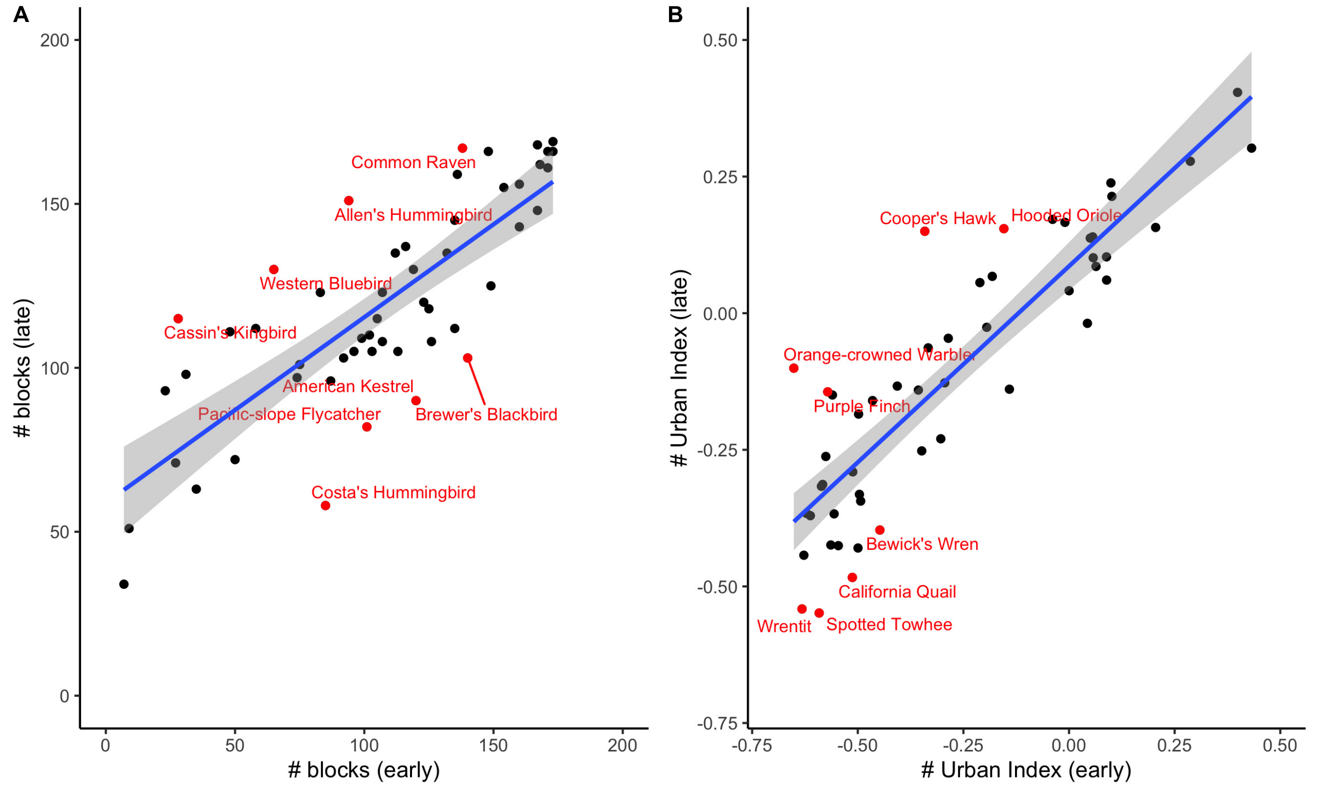

FIGURE 2 | (A) A comparison of species occurrence in early and late eras by number of blocks where suspected/confirmed breeding. **(B)** A comparison of urban index values between the early and late eras. We have labeled the species with the largest residuals from the blue best-fit line.

TABLE 2 | Comparison of three phylogenetically informed Generalized Least Squares (PGLS) models (Brownian, OU, Pagel's lambda) and one non-phylogenetically informed model (GLS).

Model	Test statistic	AICc
Early era (BBA data)		
Brownian	$K = 0.223$; $P = 0.239$ Alpha: 2.718	66.727
OU	Sigma squared: 0.544	34.391
Pagel's lambda	$L < 0.001$; $P = 1$	34.406
Non-phy.	Sigma squared: 0.001	32.151
Late era (eBird data)		
Brownian	$K = 0.189$; $P = 0.452$ Alpha: 2.718	38.826
OU	Sigma squared: 0.361	13.118
Pagel's lambda	$L < 0.001$; $P = 1$	13.099
Non-phy.	Sigma squared: 0.001	10.844

Here we use urban index scores only as our response variable (i.e., no behavioral or life history traits). The lowest AICc score was found using the non-phylogenetic model.

TABLE 3 | Comparison of AIC scores of best model (non-phylogenetic GLS) using urban index as the response variable and eight behavioral and life history traits as the predictor variables.

Model	Early era (BBA)	Late era (eBird)
Brownian	93.724	71.685
OU	66.988	51.695
Pagel's lambda	68.619	51.522
Non-phylogenetic	66.979	49.695

Full model results are available in the ***Supplementary Materials****.*

TABLE 4 | Results from the best model in both time eras (non-phylogenetic GLS) fitted to explain variation in the urban index values based on eight life history and behavioral traits (includes standard error and *P*-value).

	Early era (BBA)	Late era (eBird)
Intercept	-0.240 ± 0.161; $P = 0.142$	-0.038 ± 0.131; $P = 0.773$
Trait		
Log(adult mass)	-0.041 ± 0.041; $P = 0.330$	-0.031 ± 0.034; $P = 0.372$
Nest height	0.009 ± 0.007; $P = 0.238$	0.010 ± 0.006; $P = 0.093$
Ground-foraging	-0.070 ± 0.120; $P = 0.563$	-0.071 ± 0.098; $P = 0.471$
Migratory status	**-0.201 ± 0.099; $P = 0.047$***	-0.131 ± 0.081; $P = 0.105$
Cavity-nesting	**-0.208 ± 0.098; $P = 0.040$***	**-0.206 ± 0.080; $P = 0.014$***
Structure-nesting	**0.264 ± 0.092; $P = 0.006$***	**0.191 ± 0.075; $P = 0.014$***
Diet breadth	0.060 ± 0.038; $P = 0.135$	0.032 ± 0.031; $P = 0.301$
Habitat breadth	-0.049 ± 0.052; $P = 0.355$	-0.051 ± 0.043; $P = 0.238$
Residual standard error	0.295	0.235

Please refer to ***Supplementary Materials*** *for full model results. Asterisk and bold font denote $P < 0.05$.*

advantage (for artificial structure nesters and sedentary species) or a disadvantage (for cavity nesters and for migratory species) within urban areas, that these patterns may persist over time (even if the makeup of the species community changes) using two different data collection methodologies (i.e., a BBA dataset vs. an eBird dataset). The durability of these traits through time was suggested by Shultz et al. (2012), who found levels of functional diversity maintained in an urban bird community over a century, despite changes in community composition as the area urbanized (see also Hagen et al., 2017). Indeed, the lack of a strong phylogenetic signal in patterns we documented (in either era) suggests that urban tolerance is not restricted to a few related species, but rather occurs across unrelated taxa, as observed in both birds and other taxonomic groups (Martin and Bonier, 2018; Merckx et al., 2018; Santini et al., 2019).

The significant negative association between cavity nesting and urban index may be a result of urban tree species in urban Los Angeles having been selected for their longevity, rapid growth, and resistance to boring pests (Gutzat and Dormann, 2018; Frank et al., 2019), and the tendency for large urban trees, especially those with dead limbs ("snags") to be removed in residential areas due to safety concerns (falling branches injuring people). It may be that more successful urban nesters would be those species that are able to utilize a variety of built structures (as well as natural cavities), including eaves of buildings, parking garages, and overpasses, with this flexibility allowing them to switch between substrates when one is not available. It is also possible that aggressive (urban-tolerant) cavity nesters such as European Starlings (*Sturnus vulgaris*) and/or parrots may be displacing natural cavity nesters within urban areas, though direct evidence of this is lacking (Koch et al., 2012; Diamond and Ross, 2019). Still, avian diversity in urban areas could be enhanced by provisioning artificial nesting structures, and maintaining natural nesting sites such as dead trees (see Tomasevic and Marzluff, 2017), as well as by retaining patches of natural habitat of various sizes within the urban matrix (Silva et al., 2015) and by planting a diversity of trees and shrubs as part of landscaping (Wood and Esaian, 2020).

We found no significant correlations between urban index and body mass, ground foraging, or either diet or habitat breadth, all of which have been found to be associated with urban in prior studies (e.g., Chace and Walsh, 2006; Evans et al., 2011). It could be that the large scale of the atlas blocks (ca. 2,668 ha) encompassed a variety of habitat types and variety of urban conditions (which we did not analyze here), so a finer-level analysis (e.g., eBird point data) might detect more significant associations (see Croci et al., 2008; Ferenc et al., 2014 for discussions of scale). While not statistically significant, the consistent positive associations found between urban index and nest height may indeed be "real," as so many structure-nesting birds nest atop towers, buildings, and other tall features of the urban environment, which are less prevalent in wildland habitats and which would become more common over time in urban areas as infill hardscape development displaces vegetation (e.g., Lee et al., 2017). Likewise, the consistent negative association with migratory status across several models used, while (weakly) significant only during the early era, may become stronger with additional (migratory) species included in a future analysis (including data from multiple cities), or with finer-grain migration data (our binary "migratory status" trait does reflect the range of long- and short-distance and partial migrants).

We also note that certain species are clearly modifying their tolerance to local urbanization as they increase in distribution within the study area, which may lead to concurrent changes in their ecological traits. For example, Dark-eyed Juncos were found on roughly three times as many survey blocks in the early vs. late era, and saw their urban index shift from strongly negative in the early era (−0.56) to weakly negative by the late era (−0.15) (**Supplementary Table S1**). This species is now a year-round resident across the Los Angeles Basin, and is frequently found nesting in structures, including within parking structures in urban Los Angeles (D.S. Cooper pers. obs.); decades ago it was largely a migratory ground-nester, restricted to montane areas for breeding (Garrett and Dunn, 1981; Allen et al., 2016). Likewise, structure-nesting in Cassin's Kingbirds was not mentioned in recent breeding bird atlases based on data from the 1990s (Unitt, 2004; Allen et al., 2016), but this tendency has since become a frequent sight around Los Angeles (pers. obs.), during which time this species has increased its representation on survey blocks roughly fourfold. We encourage more research on the differential usage of cavities and artificial structures in urban areas and at the urban edge, as urban-colonizing species continue to utilize new substrates for breeding (see Reynolds et al., 2019).

Our finding that overall, species were found more widely (i.e., in more survey blocks) and with higher urban indices in the late era than the early one may be an artifact of the two different methodologies used in data collection rather than a biological pattern. This is likely a result of the more inclusive approach assigning breeding status from the (later) eBird data (where only breeding season records of single birds or pairs was used to denote breeding) versus the more conservative approach used in generating the BBA data, which required observers to justify their assessment of nesting with field observations. Thus, birds recorded only once in 5 years in a given block might not have warranted a "possibly breeding" (i.e., code 1) assignment in the early era, because these determinations were often made *post hoc* and somewhat subjectively by the atlas coordinators, based on suitable habitat, other nesting behavior, etc. (see Allen et al., 2016); yet for the late era dataset, a "one-off" sighting would have been counted as possibly breeding. Because reliable abundance data were not available for the Breeding Bird Atlas, we did not calculate abundance using the eBird data, and simply used scores between 0 and 2, summing them as a substitute for abundance across all 173 blocks. Abundance should be more easily calculated in the future as community-science projects expand and the amount of point data increases, allowing for more granular studies into local and regional biodiversity, population and range shifts, and community organization (e.g., Ballard et al., 2017; Callaghan et al., 2017; Jarić et al., 2020). Although we limited our analysis to the breeding season, when our focal bird species would likely be tied to a specific territory and thus dependent on the local resources available for themselves and their offspring (Mills et al., 1989), a similar analysis could be performed for wintering or even transient species using data collected at other times of year, a period when urban habitats are utilized by a diversity of native bird species (e.g., Wood and Esaian, 2020).

Finally, as urbanization continues to expand globally, we encourage further reflection on ways to define "success" in urban areas. On one hand, cities may be considered successful if they include built features that can support a high diversity of species, some of which would not have occurred prior to urbanization (White et al., 2005; Filazzola et al., 2019). Yet cities must also allow the least-adaptable species – those most strongly associated with wildland rather than urban habitats – to find refuge within the urban matrix as they urbanize (Sol et al., 2014). Much of this tension results from studies using different scales of analysis; high local diversity may be easier to achieve within cities than high global diversity, which requires the conservation of rare and endemic species (e.g., Enedino et al., 2018; McDonald et al., 2018). Place matters, too, and while a featureless desert may support relatively few bird species compared to the oasis-like city that replaces it (e.g., Gonzalez-Garcia et al., 2014), this scenario would hardly be considered a desirable conservation to be replicated everywhere (otherwise, why not cover the earth in cities?). Thus, an understanding of the mechanics of urban bird community development is merely a necessary first step on the way to developing meaningful conservation goals.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

DC and AS: conceptualization, methodology, and data analysis. DB: methodology and supervision. DC: Writing, including original draft. All authors: review and editing.

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SUPPLEMENTARY MATERIAL

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REFERENCES

Aldrich, J. W., and Coffin, R. W. (1980). Breeding bird populations from forest to suburbia after thirty-seven years. *Am. Birds* 34, 3–7.

Allen, L., Garrett, K. L., and Wimer, M. (2016). *Los Angeles County Breeding Bird Atlas*. Los Angeles, CA: Los Angeles Audubon Society.

Allen, L. W., and Garrett, K. L. (1995). *Atlas Handbook: Los Angeles County Breeding Bird Atlas*. Los Angeles, CA: Los Angeles Audubon Society.

Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W., and Ketterson, E. D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behav. Ecol.* 23, 960–969. doi: 10.1093/beheco/ars059

Ballard, H. B., Robinson, L. D., Young, A. N., Pauly, G. B., Higgins, L. M., Johnson, R. F., et al. (2017). Contributions to conservation outcomes of natural history museum-led citizen science: examining evidence and next steps. *Biol. Cons.* 208, 87–97. doi: 10.1016/j.biocon.2016.08.040

Beissinger, S. R., and Osborne, D. R. (1982). Effects of urbanization on avian community organization. *Condor* 84, 75–83.

Beninde, J., Veith, M., and Hochkirch, A. (2015). Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecol. Lett.* 18, 581–592. doi: 10.1111/ele.12427

Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. *Ecol. Appl.* 6, 506–519. doi: 10.2307/2269387

Blewett, C. M., and Marzluff, J. M. (2005). Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. *Condor* 107, 678–693. doi: 10.1093/condor/107.3.678

Blomberg, S. P., Garland, T., and Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57, 717–745. doi: 10.1111/j.0014-3820.2003.tb00285.x

Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Anim. Behav.* 71, 389–399. doi: 10.1016/j.anbehav.2005.05.010

Blumstein, D. T. (2014). "Attention, habituation, and antipredator behavior: implications for birds," in *Avian Urban Ecology*, eds D. Gil, and H. Brumm (Oxford: Oxford Univ. Press), 41–53. doi: 10.1093/acprof:osobl/9780199661572.003.0004

Boal, C. W., and Mannan, R. W. (1999). Comparative breeding ecology of Cooper's hawks in urban and exurban areas of southeastern Arizona. *J. Wildl. Manag.* 63, 77–84.

Bonier, F., Martin, P. R., and Wingfield, J. C. (2007). Urban birds have broader environmental tolerance. *Biol. Lett.* 3, 670–673. doi: 10.1098/rsbl.2007.0349

Callaghan, C. T., Lyons, M. B., Martin, J. M., Major, R. E., and Kingsford, R. T. (2017). Assessing the reliability of avian biodiversity measures of urban greenspaces using eBird citizen science data. *Avian Cons. Ecol.* 12:12.

CALVEG, (2009). *South Coast and Montane Ecological Province, CALVEG Zone 7*. Available at: https://www.fs.usda.gov/detail/r5/landmanagement/resourcemanagement/?cid=stelprdb5347192 (accessed August 10, 2018).

Carrete, M., and Tella, J. L. (2011). Inter-Individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PLoS One* 6:e18859. doi: 10.1371/journal.pone.0018859

Center for Geographical Studies (2015). *A Shared Vision for The Survey of California Vegetation*. Los Angeles, CA: California State University.

Chace, J. F., and Walsh, J. J. (2006). Urban effects on native avifauna: a review. *Landsc. Urb. Plan.* 74, 46–69. doi: 10.1016/j.landurbplan.2004.08.007

City of Los Angeles (2018). 2018 Biodiversity report: Measurement of the Singapore Index of Cities' Biodiversity and Recommendations for a Customized Los Angeles Index. Available at: https://www.lacitysan.org/cs/groups/public/documents/document/y250/mdi0/~{}edisp/cnt024743.pdf (accessed July 2, 2020).

Clergeau, P., Jokimäki, J., and Savard, J.-P. (2001). Are urban bird communities influenced by the bird diversity of adjacent landscapes. *J. Appl. Ecol.* 28, 1122–1134. doi: 10.1046/j.1365-2664.2001.00666.x

Croci, S., Butet, A., and Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits? *Condor* 110, 223–240. doi: 10.1525/cond.2008.8409

Devictor, V., Julliard, R., Couvet, D., Lee, A., and Jiguet, F. (2007). Functional homogenization effect of urbanization on bird communities. *Cons. Biol.* 21, 741–751. doi: 10.1111/j.1523-1739.2007.00671.x

Diamond, J. M., and Ross, M. S. (2019). Exotic parrots breeding in urban tree cavities: nesting requirements, geographic distribution, and potential impacts on cavity nesting birds in southeast Florida. *Avian Res.* 10:39.

Dunning, J. B. (2007). *CRC Handbook of Avian Body Masses*, 2nd Edn. Boca Raton, FL: CRC Press.

Ehrlich, P. R., Dobkin, D. S., and Wheye, D. (1988). *The Birder's Handbook: A Field Guide to the Natural History of North American Birds*. New York: Simon and Schuster/Fireside Books.

Emlen, J. T. (1974). An urban bird community in Tucson, Arizona: derivation, structure, regulation. *Condor* 76, 184–197.

Enedino, T. R., Loures-Ribeiro, A., and Santos, B. A. (2018). Protecting biodiversity in urbanizing regions: the role of urban reserves for the conservation of Brazilian Atlantic Forest birds. *Perspect. Ecol. Const.* 16, 17–23. doi: 10.1016/j.pecon.2017.11.001

Estes, W. A., and Mannan, R. W. (2003). Feeding behavior of Cooper's Hawks at urban and rural nests in southeastern Arizona. *Condor* 105, 107–116. doi: 10.1093/condor/105.1.107

Evans, J., Boudreau, K., and Hyman, J. (2010). Behavioral syndromes in urban and rural populations of song sparrows. *Ethology* 116, 588–595.

Evans, K. L., Chamberlain, D. E., Hatchwell, B. J., Gregory, R. D., and Gaston, K. J. (2011). What makes an urban bird? *Glob. Change Biol.* 17, 32–44. doi: 10.1111/j.1365-2486.2010.02247.x

Ferenc, M., Sedláèek, O., Fuchs, R., Dinetti, M., Fraissinet, M., and Storch, D. (2014). Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe. *Glob. Ecol. Biogeogr.* 23, 479–489. doi: 10.1111/geb.12130

Filazzola, A., Shrestha, N., and MacIvor, J. S. (2019). The contribution of constructed green infrastructure to urban biodiversity: a synthesis and meta-analysis. *J. Appl. Ecol.* 56, 2131–2143.

Francis, C. D., Ortega, C. P., and Cruz, A. (2009). Noise pollution changes avian communities and species interactions. *Curr. Biol.* 19, 1415–1419. doi: 10.1016/j.cub.2009.06.052

Frank, S. D., Backe, K. M., McDaniel, C., Green, M., Widney, S., and Dunn, R. R. (2019). Exotic urban trees conserve similar natural enemy communities to native congeners but have fewer pests. *PeerJ* 7:e6531. doi: 10.7717/peerj.6531

Garrett, K., and Dunn, J. (1981). *Birds of Southern California: Status and Distribution*. Los Angeles, CA: Los Angeles Audubon Society.

Garrett, K. L. (2018). "Introducing change: a current look at naturalized bird species in western North America in Trends and traditions: avifaunal change in western North America," in *Studies of Western Birds 3*, eds W. D. Shuford, R. E. Gill, Jr., and C. M. Handel, (Camarillo, CA: Western Field Ornithologists), 116–130. doi: 10.21199/swb3.5

Gillespie, T. W., Pincetl, S., Brossard, S., Smith, J., Saatchi, S., Pataki, D., et al. (2011). A time series of urban forestry in Los Angeles. *Urb. Ecosyst.* 15, 233–246. doi: 10.1007/s11252-011-0183-6

Gonzalez-Garcia, F., Straub, R., Lobato Garcia, J. A., and MacGregor-Fors, I. (2014). Birds of a neotropical green city: an up-to-date review of the avifauna of the city of Xalapa with additional unpublished records. *Urb. Ecosyst.* 17, 991–1012. doi: 10.1007/s11252-014-0370-3

Grinnell, J. (1898). *Birds of the Pacific slope of Los Angeles County*. Pasadena, NL: Pasadena Academy of Sciences.

Gutzat, F., and Dormann, C. (2018). Decaying trees improve nesting opportunities for cavity-nesting birds in temperate and boreal forests: a meta-analysis and implications for retention forestry. *Ecol. Evol.* 8, 8616–8626. doi: 10.1002/ece3.4245

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., et al. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science* 320, 1763–1768.

Hagen, E. O., Hagen, O., Ibáñez-Álamo, J. D., Petchey, O. L., and Evans, K. L. (2017). Impacts of urban areas and their characteristics on avian functional diversity. *Front. Ecol. Evol.* 5:84. doi: 10.3389/fevo.2017.00084

Harrell, F. E. (2004). *Hmisc S Function Library*. Available at: http://biostat.mc.vanderbilt.edu/s/Hmisc (accessed October 22, 2019).

Higgins, L., Pauly, G. B., Goldman, J. G., and Hood, C. (2019). *Wild LA*. Portland: Timber Press.

Horns, J. J., Alder, F. R., and Sekercioglu, C. H. (2018). Using opportunistic citizen science data to estimate average population trends. *Biol. Constr.* 221, 151–159. doi: 10.1016/j.biocon.2018.02.027

Iacus, S. M. (2016). *sde: Simulation and Inference for Stochastic Differential Equations. R package version 2.0.15*.

Jarić, I., Correia, R. A., Brook, B. W., Buettel, J. C., and Roll, U. (2020). iEcology: harnessing large online resources to generate ecological insights. *TREE* 35, 630–639. doi: 10.1016/j.tree.2020.03.003

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., and Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature* 491, 444–448. doi: 10.1038/nature11631

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., Redding, D., and Mooers, A. O. (2014). Distribution and conservation of global evolutionary distinctness in birds. *Curr. Biol.* 24, 919–930. doi: 10.1016/j.cub.2014.03.011

Johnston, R. F. (2001). "Synanthropic birds of North America," in *Avian Ecology and Conservation in an Urbanizing World*, eds J. M. Marzluff, R. Bowman, and R. Donnelly, (Boston, MA: Springer), 49–67. doi: 10.1007/978-1-4615-1531-9_3

Jokimäki, J., Suhonen, J., Vuorisalo, T., Kover, L., and Kaisanlahti-Jokimäki, J. (2017). Urbanization and nest-site selection of the black-billed magpie (Pica pica) populations in two Finnish cities: from a persecuted species to an urban exploiter. *Landsc. Urb. Plan.* 157, 577–585. doi: 10.1016/j.landurbplan.2016.08.001

Kark, S., Iwaniuk, A., Schalimtzek, A., and Banker, E. (2007). Living in the city: can anyone become an 'urban exploiter'? *J. Biogeogr.* 34, 638–651. doi: 10.1111/j.1365-2699.2006.01638.x

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, S. P., et al. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26, 1463–1464. doi: 10.1093/bioinformatics/btq166

Kettel, E. F., Gentle, L. K., Quinn, J. L., and Yarnell, R. W. (2018). The breeding performance of raptors in urban landscapes: a review and meta-analysis. *J. Ornithol.* 159, 1–18. doi: 10.1007/s10336-017-1497-9

Koch, A. J., Martin, K., and Aitken, K. E. H. (2012). The relationship between introduced European Starlings and the reproductive activities of Mountain Bluebirds and Tree Swallows in British Columbia, Canada. *IBIS* 154, 590–600. doi: 10.1111/j.1474-919x.2012.01242.x

Lee, S. J., Longcore, T. L., Rich, C., and Wilson, J. P. (2017). Increased home size and hardscape decreases urban forest cover in Los Angeles County's single-family residential neighborhoods. *Urb. Forestry Urb. Greening* 24, 222–235. doi: 10.1016/j.ufug.2017.03.004

Li, E., Parker, S. S., Pauly, G. B., Randall, J. M., Brown, B. V., and Cohen, B. S. (2019). An urban biodiversity assessment framework that combines an urban habitat classification scheme and citizen science data. *Front. Ecol. Evol.* 7:277. doi: 10.3389/fevo.2019.00277

Los Angeles Almanac, (2019). *Historical General Population, City & County of Los Angeles, 1850 to 2010." Los Angeles Almanac. Copyright 1998-2019 Given Place Media, publishing as Los Angeles Almanac*. Available at: http://www.laalmanac.com/population/po02.php (accessed 5 December 2019).

Loss, S. R., Will, T., and Marra, P. P. (2013). The impact of free ranging domestic cats on wildlife of the United States. *Nat. Commun.* 4:1396.

Lowry, H., Lill, A., and Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549. doi: 10.1111/brv.12012

MacGregor-Fors, I. (2010). How to measure the urban-wildland ecotones: Redefining 'peri-urban' areas. *Ecol. Res.* 25, 883–997.

MacGregor-Fors, I., and Ortega-Alvarez, R. (2011). Fading from the forest: bird community shifts related to urban site-specific and landscape traits. *Urb. Forestry Urb. Greening* 10, 239–246. doi: 10.1016/j.ufug.2011.03.004

Martin, P. R., and Bonier, F. (2018). Species interactions limit the occurrence of urban-adapted birds in cities. *PNAS* 115, E11495–E11504.

Martins, E. P. (1994). Estimating the rate of phenotypic evolution from comparative data. *Am. Nat.* 144, 193–209. doi: 10.1086/285670

Marzluff, J. M. (2005). Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. *Urb. Ecosyst.* 8, 157–177. doi: 10.1007/s11252-005-4378-6

Marzluff, J. M. (2016). A decadal review of urban ornithology and prospectus for the future. *IBIS* 159, 1–13. doi: 10.1111/ibi.12430

Marzluff, J. M., Bowman, R., and Donnely, R. (2001). "A historical perspective on urban bird research: trends, terms, and approaches," in *Avian Conservation and Ecology in an Urbanizing World*, eds J. M. Marzluff, R. Bowman, and R. Donnely, (Boston, MA: Kluwer Academic), 1–17. doi: 10.1007/978-1-4615-1531-9_1

Marzluff, J. M., Clucas, B., Oleyar, M. D., and DeLap, J. (2015). The causal response of avian communities to suburban development: a quasi-experimental, longitudinal study. *Urb. Ecosyst.* 19, 1597–1621. doi: 10.1007/s11252-015-0483-3

McDonald, R. I., Güneralp, B., Huang, C.-W., Seto, K. C., and You, M. (2018). Conservation priorities to protect certebrate endemics from global urban expansion. *Biol. Constr.* 224, 290–299. doi: 10.1016/j.biocon.2018.06.010

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biol. Constr.* 127, 247–260. doi: 10.1016/j.biocon.2005.09.005

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L. F., Backeljau, T., Bonte, D., et al. (2018). Body-size shifts in aquatic and terrestrial urban communities. *Nature* 558, 113–116.

Mills, G. S., Dunning, J. B. Jr., and Bates, J. M. (1989). Effects of urbanization on breeding bird community structure in southwestern desert habitats. *Condor* 91, 416–428.

Møller, A. P. (2009). Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia* 159, 849–858. doi: 10.1007/s00442-008-1259-8

Møller, A. P. (2010). Interspecific variation in fear responses predicts urbanization in birds. *Behav. Ecol.* 21, 365–371. doi: 10.1093/beheco/arp199

Møller, A. P. (2014). "Behavioral and ecological predictors of urbanization," in *Avian Urban Ecology*, eds D. Gil, and H. Brumm, (Oxford: Oxford Univ. Press), 54–68. doi: 10.1093/acprof:osobl/9780199661572.003.0005

Møller, A. P., Diaz, M., Flensted-Jensen, E., Grim, T., Ibanez-Alamo, J. D., Jokimäki, J., et al. (2015). Urbanized birds have superior establishment success in novel environments. *Oecologia* 178, 943–950. doi: 10.1007/s00442-015-3268-8

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., et al. (2012). How to measure and test phylogenetic signal. *Method Ecol. Evol.* 3, 743–756. doi: 10.1111/j.2041-210x.2012.00196.x

O'Leary, R., and Jones, D. N. (2006). The use of supplementary foods by Australian magpies *Gymnorhina tibicen*: implications for wildlife feeding in suburban environments. *Austral. Ecol.* 31, 208–216. doi: 10.1111/j.1442-9993.2006.01583.x

Pagel, M. D. (1999). Inferring the historical patterns of biological evolution. *Nature* 401, 877–884. doi: 10.1038/44766

Paradis, E., Claude, J., and Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290. doi: 10.1093/bioinformatics/btg412

Pauli, B. P., Spaul, R. J., and Heath, J. A. (2016). Forecasting disturbance effects on wildlife: tolerance does not mitigate effects of increased recreation on wildlands. *Anim. Constr.* 20, 251–260. doi: 10.1111/acv.12308

Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., Uyeda, J. C., FitzJohn, R. G., et al. (2014). geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* 30, 2216–2218. doi: 10.1093/bioinformatics/btu181

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team, (2019). *nlme: Linear and Nonlinear Mixed Effects Models. R Pack. Vers. 3.1-143*.

QGIS Development Team, (2016). *QGIS Geographic Information System. Open Source Geospatial Foundation Project*. Available at: http://qgis.osgeo.org (accessed September 4, 2019).

Revell, L. J. (2012). Phytools: an R package for phylogenetic comparative biology (and other things). *Method Ecol. Evol.* 3, 217–223. doi: 10.1111/j.2041-210x.2011.00169.x

Reynolds, S. J., Ibáñez-Álamo, J. D., Sumasgutner, P., and Mainwaring, M. C. (2019). Urbanisation and nest building in birds: a review of threats and opportunities. *J. Ornith.* 160, 841–860. doi: 10.1007/s10336-019-01657-8

Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F., and Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. *Nat. Commun.* 6:8877.

Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., Von Hardenberg, A., and Ancillotto, L. (2019). One strategy does not fit all: determinants of urban adaptation in mammals. *Ecol. Lett.* 22, 365–376. doi: 10.1111/ele.13199

Santos, M. J., Smith, A. B., Thorne, J. H., and Moritz, C. (2017). The relative influence of change in habitat and climate on elevational range limits in small mammals in Yosemite National Park, California, U.S.A. *Clim. Change Responses* 4:7.

Schoenherr, A. A. (1992). *A Natural History of California. California Natural History Guides: 56*. Berkeley, CA: Univ. of California Press.

Shultz, A. J., Tingley, M. W., and Bowie, R. C. K. (2012). A century of avian community turnover in an urban green space in northern California. *Condor* 114, 258–267. doi: 10.1525/cond.2012.110029

Silva, C. P., García, C. E., Estay, S. A., and Barbosa, O. (2015). Bird richness and abundance in response to urban form in a Latin American city: valdivia, Chile as a case study. *PLoS One* 10:e0138120. doi: 10.1371/journal.pone.0138120

Slabbekoorn, H., and den Boer-Visser, A. (2006). Cities change the songs of birds. *Curr. Biol.* 16, 2326–2331. doi: 10.1016/j.cub.2006.10.008

Sol, D., Gonzalez-Lagos, C., Lapiedra, O., and Diaz, M. (2017). "Why are exotic birds so successful in urbanized environments?," in *Ecology and Conservation of Birds in Urban Environments*, eds E. Murgui, and M. Hedblom, (Boston, MA: Springer), 75–89. doi: 10.1007/978-3-319-43314-1_5

Sol, D., González-Lagos, C., Moreira, D., Maspons, J., and Lapiedra, O. (2014). Urbanisation tolerance and the loss of avian diversity. *Ecol. Lett.* 17, 942–950. doi: 10.1111/ele.12297

Sol, D., Lapiedra, O., and González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Anim. Behav.* 85, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Stein, E. D., Dark, S., Longcore, T., Hall, N., Beland, M., Grossinger, R., et al. (2007). *Historical Ecology and Landscape Change of the San Gabriel River and Floodplain*. Costa Mesa, CA: Southern California Coastal Water Research Project.

Swarth, H. S. (1900). Avifauna of a 100-acre ranch. *Condor* 2, 14–16. doi: 10.2307/1361152

Tomasevic, J. A., and Marzluff, J. M. (2017). Cavity nesting birds along an urban-wildland gradient: is human facilitation structuring in the bird community? *Urb. Ecosyst.* 20, 435–448. doi: 10.1007/s11252-016-0605-6

Unitt, P. (2004). *San Diego County Bird Atlas*. El Cajon, CA: Sunbelt Publications.

Vitousek, P. M., Mooney, H. A., Lubchenco, J., and Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science* 277, 494–499. doi: 10.1126/science.277.5325.494

West-Eberhard, M. J. (1989). Phenotypic plasticity and the origins of diversity. *Ann. Rev. Ecol. Syst.* 20, 249–278.

White, J. G., Antos, M. J., Fitzsimons, J. A., and Palmer, G. C. (2005). Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation. *Landsc. Urb. Plan.* 71, 123–135. doi: 10.1016/j.landurbplan.2004.02.006

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., and Jetz, W. (2014). EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* 95:2027. doi: 10.1890/13-1917.1

Wingfield, J. C., Krause, J. S., Perez, J. H., Chmura, H. E., Németh, Z., Word, K. R., et al. (2015). A mechanistic approach to understanding range shifts in a changing world: what makes a pioneer? *Gen. Comp. Endocrinol.* 222, 44–53. doi: 10.1016/j.ygcen.2015.08.022

Wood, E. M., and Esaian, S. (2020). The importance of street trees to urban avifauna. *Ecol. Applic.* (accessed July 19, 2020).

Yeh, P. J. (2004). Rapid evolution of a sexually selected trait following population establishment in a novel habitat. *Evolution* 58, 166–174. doi: 10.1111/j.0014-3820.2004.tb01583.x

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It's Not Easy Being Green: Behavior, Morphology, and Population Structure in Urban and Natural Populations of Green Anole (*Anolis carolinensis*) Lizards

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Selection on behavior, signaling, and morphology can be strongly affected by variation in habitat type. Consequently, populations inhabiting different environments can exhibit divergent phenotypes as a result of either habitat-specific selection or plasticity. Urban habitats in particular represent different challenges for organisms adapted for rural environments, including disparate complements of predators and competitors, resource availability, and habitat complexity. In this paper, I review work aimed at understanding the different selective challenges experienced by rural and urban populations of green anole lizards, primarily those in southeastern Louisiana. I also describe a long-term mark-recapture experiment on an urban population of green anoles in New Orleans, and consider how sex ratios and population density changes over time. Collectively, this work shows that urban and rural populations of green anoles diverge markedly in behavior and morphology driven both by differences in habitat and the presence of competitors in the urban environment; however, it also shows that the effects of urbanization on the ecology and evolution of green anoles are understudied.

Keywords: *Anolis*, urban ecology, behavior, morphology, habitat

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INTRODUCTION

A key principle in evolutionary biology is that environmental differences among populations can drive divergent selection on morphology, behavior, and physiology. Whether mediated by plasticity or by a genetic response to selection, phenotypes of organisms can vary markedly across populations in response to local conditions (Reznick et al., 1990; Donihue et al., 2018; Lapiedra et al., 2018). Although the nature of the divergence is determined by the specific environmental challenges in conjunction with the evolutionary history of the species or population in question, we can nonetheless discern broad patterns of repeated evolutionary change in response to similar selection pressures (Langerhans and DeWitt, 2004; Losos, 2011; Moore et al., 2016; Auer et al., 2018).

Urban environments comprise a specific habitat milieu that is characterized by distinct structural habitat and environmental variables such as light or thermal regime, amongst others. These urban environments frequently differ markedly from the natural habitats and environments of the organisms inhabiting urban areas. Additionally, because urban areas are also typified by high degrees of disturbance, as well as the presence of man-made structures, urban environments tend to exhibit greater variation in both habitat type and in the thermal microhabitat compared to natural environments (Ackley et al., 2015), but also greater habitat loss concomitant with a high degree of habitat fragmentation resulting in uneven and patchy distribution of vegetation in particular (Watling and Donnelly, 2006; Liu et al., 2016). Because urbanization results in repeated environments that are more similar to each other than they are to neighboring environments, the urban environment is in many respects a replicated one that is likely to exert many similar selection pressures on organisms that inhabit them (Delaney et al., 2010; Johnson and Munshi-South, 2017). Given the pace and scale of anthropogenic induced habitat alteration, understanding how those pressures affect the integrated overall phenotype of urban animal populations should be a priority.

An increasing number of studies are documenting distinct shifts in the phenotypes of urban populations of animals relative to their rural conspecifics. For example, urban populations of *Podarcis muralis*, a widespread lacertid lizard, exhibit greater fluctuating asymmetry in morphology than rural populations (Lazic et al., 2013). Similarly, urbanization drives genetically based differences in swimming kinematics in the fish *Semotilus atromaculatus* (Kern and Langerhans, 2019). In addition to morphology and physiology, urban conditions also affect a suite of behavioral traits ranging from acoustic signaling (Slabbekoorn and Peet, 2003; Parris et al., 2009; Luther et al., 2016) to boldness (Atwell et al., 2012) and foraging behavior (Rhodes and Catterall, 2008). Behavior is of particular interest in this regard because behavioral responses of animals to novel conditions can often precede or buffer changes in performance or morphology (Huey et al., 2003; Munoz and Losos, 2018). Indeed, behavioral flexibility is considered a hallmark of urban populations, and may lead to the breakdown of behavioral syndromes seen in natural populations (Scales et al., 2011).

Lizards are commonly found in urban environments and have emerged as a useful taxon for testing the effects of urbanization on ecology, morphology, physiology, and behavior. For instance, geckos have been touted as indicators of urban pollution and habitat quality (Fletcher et al., 2008) and the distribution of some gecko species tracks urbanization because they forage close to artificial lights where insect abundance is typically high (Zozaya et al., 2015). *Anolis* lizards in particular have previously been suggested to be ideal organisms for understanding adaptation to urban environments at multiple levels of organization, from the within- and among-individual levels to that of the species (Lapiedra, 2018), and indeed a growing number of studies have tested for adaptation to urban habitats in several species of anoles (Campbell-Staton et al., 2020).

Green anole (*Anolis carolinensis*) lizards colonized the continental United States from Cuba 12–6 million years ago (Glor et al., 2005). Over the last 100,000 years in particular, green anoles have expanded northward and westward from their original site of arrival in Florida (Bourgeois and Boissinot, 2019) and today are widely distributed from Texas in the west to Tennessee in the north, along with introduced populations in southern California, and have also been introduced on Hawai'i, Guam, and Okinawa. Importantly, *A. carolinensis* are present in both rural and urban settings across much of their North American range, often existing in researchers' literal backyards. A number of studies of green anoles consequently have used, and continue to use, individuals sampled from or present in urban habitats due to their availability (e.g., Ruby, 1984; Irschick et al., 2006b; Lailvaux et al., 2015). This makes them a useful species for comparing and testing aspects of behavior, morphology, and related traits in different environmental contexts. However, despite being the most well-studied member of the *Anolis* genus (see Lovern et al., 2004 for a historical overview), no studies yet have synthesized the literature on green anole behavioral ecology with an eye toward understanding how the urban environment in particular affects ecology, behavior, and morphology in this species.

In this paper, I review the literature on green anole urban ecology by comparison wherever possible to natural/rural populations or similar studies on such populations. I focus especially on studies comparing green anoles from two populations in southeastern Louisiana region, namely a rural and an urban population, for two main reasons. First, this body of work represents a detailed comparison of the ecology, morphology, and behavior of urban and rural green anoles in the same area and over a relatively short span of time from several diverse approaches (e.g., habitat use, sexual selection, and interspecific competition, amongst others); yet despite the broad nature of this work, it was not conducted explicitly within the emerging urban ecology framework, and was instead couched as a series of studies of intraspecific variation. Consequently, it has yet to be integrated and interpreted from an urban ecology perspective. Second, replicates of both urban and rural populations in the same region and elsewhere are for the most part unavailable, and few other studies have examined similar issues relating to morphology, performance, and (especially) behavior in other populations of green anoles, although I highlight and discuss those that have.

The ecomorphological paradigm states that morphology determines performance, and further that behavior and performance interact to determine fitness (Arnold, 1983; Garland and Losos, 1994). Consequently, I deal first with the difference in structural habitat between wild/rural and urban environments and how those differences affect morphology and performance before considering further population differences in escape and display behavior within the context of population ecology. Finally, given the paucity of long-term studies on basic aspects of urban population ecology, I present some novel data drawn from a 5-year study of another urban population in New Orleans with the aim of testing some classic hypotheses regarding temporal variation in population structure within an urban setting.

Habitat Use, Morphology, and Performance

Animals in urban areas experience clear differences in the type and availability of structural habitat compared to their natural milieu (Sol et al., 2013). These differences in habitat type can have functional consequences for both how organisms using such habitats are shaped, and how well they are able to execute dynamic, ecologically relevant tasks such as jumping, running, and biting (collectively termed whole-organism performance traits; Bennett and Huey, 1990; Lailvaux and Irschick, 2006), as well as for their behavior. *Anolis* lizards in general exemplify the interplay among habitat use, morphology, and performance whereby the match between limb length and perch diameter is mediated by behavior, resulting in lizards avoiding substrates on which their sprint performance is submaximal (Irschick and Losos, 1999). Given this "habitat constraint" phenomenon, one might predict that structural habitat differences in the urban environment will alter the morphology of urban green anole populations as well as, potentially, their performance.

The degree to which urban populations of animals might diverge in morphology and performance from conspecifics in wild populations likely depends in part on the degree of urbanization. All urban environments are characterized by increased disturbance, presence of man-made structures, and increased human foot traffic relative to wild or rural counterparts at a minimum, but there is likely to be variation in each of these even within an urbanized region. Similarly, different taxa could be differentially affected by or sensitive to urbanization (Markovchick-Nicholls et al., 2008). For example, a population of lizards in a city block or university campus might be considered to be highly urbanized in terms of the types of habitat they use and the availability and openness of that habitat relative to a natural or rural population, with a city park perhaps falling somewhere between those two extremes, whereas parks and campuses might be more similar to each other from the perspective of a different organism which uses available habitat in a different way (see also Battles et al., 2013 for a classification based on degree of disturbance).

Irschick et al. (2005a) studied two green anole populations in south-eastern Louisiana situated 30 km apart: Good Hope Field (GHF), a relatively undisturbed lowland freshwater swamp in St. Charles Parish, LA; and Tulane University campus (TU) in Orleans Parish, LA. The two sites differ markedly in habitat complexity and in the type of available habitat, with GHP dominated by tall and continuous closed habitat comprising primarily narrow perches, whereas the habitat at TU is fragmented and open, made up mainly of clumps of broad leafed palmetto (*Aspidistra elatior*) plants close to the ground but with few large trees or bushes. The habitat use of green anoles at these two sites reflected the difference in habitat availability, with 71% of TU lizards perching on palmetto leaves which are patchily distribution, as opposed to GHF lizards who perched primarily on branches (68%) and tree trunks (18%) (Irschick et al., 2005a). Importantly, however, habitat use differed significantly from random habitat availability in both populations, meaning that the anoles did not passively track the underlying habitat distribution. This difference in habitat use was also reflected in a difference in morphology, with TU lizards exhibiting a more slender body shape; longer forelimbs; shorter hindlimbs; and larger toepad areas than GHF animals (Irschick et al., 2005a). This difference in toepad area is also significant in terms of whole-organism performance, because larger toepads translated into higher clinging forces in TU lizards, possibly driven by the smoother perch substrates used by animals in this population (Irschick et al., 2005a).

The finding that green anole lizards exhibit shorter hindlimbs in habitats that have been subject to human disturbance has been replicated elsewhere in the southeastern United States. In a study comparing populations of green anoles among plots that differed in habitat type in Palmetto State Park in Texas, Dill et al. (2013) found that green anole adult females inhabiting a predominately narrow-perch habitat plot that had been subject to moderate human disturbance (i.e., the Lake plot; see Battles et al., 2013) also had shorter hindlimbs than females from natural plots, whereas males exhibited no such difference. In this case, the limb morphology difference tracks the habitat use, unlike the TU lizards which have shorter hindlimbs despite using broader perches (Irschick et al., 2005a). Dill et al. (2013) further noted that this difference arises only in adults, with juveniles showing no effects of population on limb morphology. These sex- and age-specific effects are consistent with a causal explanation of plasticity driving the population effect, as opposed to selection, particularly since green anole females are known to be more plastic in their limb morphology than males (Kolbe and Losos, 2005).

Subsequent studies of urban populations using other *Anolis* species have reported very similar patterns to those exhibited by green anoles. For example, urban *Anolis cristatellus* and *Anolis sagrei* lizards prefer broader perches (Battles et al., 2018) and also exhibit longer limbs (albeit again hindlimbs as opposed to forelimbs) than their rural counterparts (Marnocha et al., 2011; Winchell et al., 2016). Furthermore, urban *A. cristatellus* also exhibit larger toepad areas, just as urban green anoles do (Winchell et al., 2016), and thus likely higher clinging ability as well. Despite these patterns, Kolbe et al. (2016) noted that *A. cristatellus* lizards in urban habitats do not conform to the habitat constraint hypothesis, frequently making use of structural habitat substrates on which sprint performance is not maximized (see also Winchell et al., 2018a; Winchell et al., 2018b). It is unclear whether urban green anoles exhibit the same phenomenon, although Gilman and Irschick (2013) found that green anoles in a park in Volusia County, Florida, preferred to jump from low compliance perches, and avoided compliant perches that are known to impede jumping ability (Gilman et al., 2012). However, despite the urban setting of this population the distribution of available habitat is more similar to that of the rural GHP population in Louisiana. Furthermore, given that the performance phenotype is a multivariate one and different performance traits are supported by different morphologies it is likely that habitat choice involves trade-offs among different aspects of performance such as sprinting, jumping, and endurance (Husak and Lailvaux, 2019; Lailvaux et al., 2019), and that these trade-offs are different in urban versus natural environments (see Winchell et al., 2018b for an example). Consequently, habitat constraint could be context-dependent.

In addition to direct effects on morphology, changes in habitat due to human activity can also have indirect effects on lizard shape and size. Battles et al. (2013) found the body condition (assessed specifically via a body-mass index measure) of female green anoles to be higher in natural plots compared to disturbed ones in Palmetto State Park, TX. Even though arthropod biomass was also higher in natural plots, these differences did not appear to be driven by prey availability but likely have complex causes including, potentially, habitat sensitivity (Battles et al., 2013). This complexity appears to extend to other *Anolis* species as well; for example, Hall and Warner (2017) found the opposite pattern in *A. cristatellus* lizards in south Florida, with *A. cristatellus* from an urban site exhibiting higher body condition than those from a forested site, yet Chejanovski et al. (2017) found no effect at all of urbanization on body condition in *A. cristatellus* within their native range in Puerto Rico, but did find higher condition in urban *A. sagrei* lizards compared to those from natural populations. Finally, Winchell et al. (2019) found that body condition does vary between urban and natural populations of *A. cristatellus* in Puerto Rico, albeit not always in a consistent direction. The mechanisms underlying these changes in condition are unclear, and it is worth noting that morphological condition indices have often been criticized, and that their functional and ecological relevance is controversial (Vervust et al., 2008; but see Husak and Lailvaux, 2019).

Escape Behavior

Although lizards will not necessarily make use of all of the habitat available to them (Johnson et al., 2006), this variation can nonetheless drive differences in behavior in specific ecological contexts. One such behavior that is affected by habitat type and availability is escape behavior. The decision as to when to flee from a potential threat weighs the various opportunity and energetic costs of escape against the probability of mortality (Ydenberg and Dill, 1986; Cooper, 2015b). These costs are themselves dependent on numerous intrinsic and extrinsic factors including habitat type and openness (Martin and López, 1995); temperature (in ectotherms) (Hertz et al., 1982); sex (Lailvaux et al., 2003); and the presence of humans (Mikula, 2014). That urban populations of birds allow closer approach of humans before initiating escape compared to rural ones has been attributed to habituation to human presence (Cooke, 1980; Blumstein, 2014).

Good Hope Field and TU lizards also show significant differences in escape behavior. A finding common to both populations is that males allow closer approach to a potential predator than females before initiating escape, although there was no effect of either sex or population on how far lizards fled; however, both male and female GHP anoles showed significantly longer approach distances than TU lizards (Irschick et al., 2005a). McMillan and Irschick (2010) used clay models to measure predation pressures at these same two populations and found no evidence of attacks by predators at the urban TU site, but a much higher frequency of bites from predators on models in the GHF swamp locality. This suggests that TU green anoles likely allow closer approach of human "predators" before initiating flight because they are habituated to the presence of humans; indeed, flight initiation distance is substantially shorter in habituated compared to unhabituated populations in eleven lizard species spanning six families (Cooper, 2015a), as well as in other anoles (Avilés-Rodríguez and Kolbe, 2019). Although the TU escape behavior results are consistent with this literature, the findings of McMillan and Irschick (2010) regarding low predation pressure in the urban TU population stands in contrast to similar studies on related lizards. For example, Tyler et al. (2016) used frequency of tail autotomy in the congener *Anolis cristatellus* as a proxy for predation pressure in urban and natural sites in four areas of Puerto Rico, and found that urban populations exhibited consistently higher frequencies of tail autotomy and regeneration, pointing toward clear differences in the predation ecology, be it predator density or efficiency, of the two population types (a further possibility is competition; see below). McMillan and Irschick (2010) did not consider autotomy in their study, and it could be that clay models and autotomy frequency capture different aspects of predation ecology. Interspecific variation in response to the threat of predation is yet another possibility (Blumstein et al., 2005; Vanhooydonck et al., 2007).

One feature of urban ecology that might mediate results gleaned from these different approaches to estimating predation is boldness, which describes the behavioral response to threatening situations. Boldness can be selected against by predation pressure (Lapiedra et al., 2018), but may also be a common feature of urban populations of organisms (Lowry et al., 2013); indeed, there is evidence that increased boldness and exploratory behavior is associated with populations inhabiting novel urban habitat in various animals (Evans et al., 2010; Atwell et al., 2012; but see Hurtado and Mabry, 2017; Sol et al., 2018), including several species of lizards (Damas-Moreira et al., 2019; but see Putnam et al., 2020). Kuo et al. (2015) found that bolder *Anolis sagrei* individuals more readily autotomize their tails, and also exhibited a higher propensity to drop their tails when available food resources are abundant. If bolder individuals are more likely to persist in urban areas with ample resources, then those individuals might exhibit higher frequencies of tail autotomy independent of predation risk. For example, Itescu et al. (2017) found that tail loss was a function of intraspecific competition rather than predation in two species of Mediterranean geckos. Habitat type has also been suggested as a potential factor (Bateman and Fleming, 2009). Of course neither clay models nor autotomy frequency are perfect indices of predation, and it may well be the case that there are key differences in the predation ecology of the urban environments in Puerto Rico versus southeastern Louisiana. Furthermore, no studies to my knowledge have considered boldness and autotomy in urban green anoles. However, given the general higher population densities of lizards in urban versus natural populations (see below) as well as the general differences in structural habitat, the notion that boldness affects tail loss of anoles in urban environments via avenues other than predation is a testable hypothesis.

Display Behavior, Population Density, and Parasitism

Natural selection favors displays, signals, and receptors that maximize signal to noise ratio in a given environment (Endler, 1992). Because the physical properties of the environment can affect signal transmission and degradation, signaling behavior can also be modulated by microhabitat choice and availability

(Calsbeek and Marnocha, 2006; Barker and Mennill, 2009). Consequently, differences in structural habitat can also drive divergence in display behavior between urban and natural animal populations (Fernández-Juricic et al., 2005). *Anolis* lizards communicate via visual displays involving stereotyped movements of the head and the dewlap, an extensible flap of colorful skin under the throat (Fleishman, 1992). Males will display toward other males, females, and potential predators but will also perform undirected displays that appear to advertise territory ownership. Although variable both within and among species, displays in green anoles are highly conserved and feature at least three distinct combinations of head bobs and dewlap extensions, termed A, B, and C displays, respectively (Lovern et al., 1999; Lovern and Jenssen, 2003; Orrell and Jenssen, 2003). Juveniles and adult females also perform versions of these displays, despite their reduced dewlap size (Lovern and Jenssen, 2003).

Although the structure of these displays is remarkably stable, both display rate and the proportions of display types can vary among populations. Bloch and Irschick (2006) compared display behavior of green anoles at the urban TU and rural GHF sites and found that Tulane anoles not only displayed roughly twice as much as GHF anoles, they also differed significantly in their relative frequencies of display types: TU lizards exhibited higher proportions of A and B display types, whereas C type displays were observed more often in rural GHF. However, there was also evidence of a previously undescribed display type, termed the Y display, in GHF but not in the TU population (Bloch and Irschick, 2006). Although this suggests that the urban environment might constrain display behavior, this difference could also arise due to some factor that is only indirectly related or entirely unrelated to urbanization. For example, Edwards and Lailvaux (2012) studied the display behaviors of two different green anole populations within the greater New Orleans area, and found that proportions of display types were altered by both habitat type and the presence of an invasive congener (*A. sagrei*).

Invasive species are a perennial feature of urban environments (Blair, 2001). Just as the urban habitat is a replicated one, so urbanization also leads to biotic homogenization and a loss of diversity in species assemblages (McKinney, 2006) as urban intolerant natives are replaced with successful invaders. One mechanism for this may be alteration of habitat in urban and disturbed areas, which can exclude native species from the modified urban environment (Forman, 2014). Indeed the loss of habitat complexity alone in urban areas can contribute to a decline in density of native species; for example, Petren and Case (1998) showed that experimentally increasing structural habitat complexity reduced interspecific competition between an invasive and a non-invasive gecko species. These collective effects of biotic homogenization and decreased complexity and diversity of structural habitat could exert significant selection on the behaviors of local native species.

One common characteristic of successful invasive species is that they often exist at higher population densities in invasive areas compared to within their native range. For example, population densities of *Eleutherodactylus coqui* frogs are estimated to be three times denser on Hawai'i, where they are invasive, compared to native populations on Puerto Rico (Woolbright et al., 2006). Consequently, a further indirect consequence of invasive species presence which can also affect native behavior is a negative effect on population density of natives. Bloch and Irschick (2006) reported a density of 0.19 males/m^2 at the urban TU population at time of their study (2004). However, Edwards and Lailvaux (2012) estimated the male density of that same population in 2010 to be 0.073 males/m^2; less than half of the population density 6 years earlier. Furthermore, the total display time of males at the TU population was also roughly halved compared to that reported earlier by Bloch and Irschick (2006). The major difference between the TU population of 2004 and the same population of 2010 is the presence of *A. sagrei*, which was absent from TU at the time of the earlier study (Edwards and Lailvaux, 2012; SPL personal observation). Indeed, Bloch and Irschick (2006) specifically noted that the TU male density was stable at the time they undertook their initial study. Furthermore, *A. sagrei* is known to exist at remarkably high densities elsewhere within its range, habitat permitting, even when other anoles are present (Schoener and Schoener, 1980). Taken together, the results of these two studies suggest that the establishment of *A. sagrei* on TU campus affected the density of green anole males in that population, either by limiting the amount of habitat available to those males which in turn altered their habitat use (Edwards and Lailvaux, 2012) or by altering the habitat use of green anole females, which prompted males to follow suit (Edwards and Lailvaux, 2013). The replicated nature of these challenges in urban environments strongly suggests that green anoles in other areas are likely to face similar challenges when faced with the presence of invasive *A. sagrei* in particular.

Although the presence of *A. sagrei* appears to have had a negative effect on the density of *A. carolinensis* males at TU in 2010, there is also evidence that green anole male TU density in 2004 was already artificially high - almost three times higher compared to rural GHF (Bloch and Irschick, 2006). This increased density can have implications for intraspecific behavioral interactions. For instance, in addition to a low (or absent) predator density at TU relative to GHF, the clay model approach of McMillan and Irschick (2010) also revealed that TU lizards seemed to experienced intense male-male competition, as all of the model bites on TU campus were inflicted by green anole males. This competition was significantly higher than that at the GHP locality based on the same index, and also exhibited a clear temporal component, with competition appearing more intense at both GHF and TU during the anole breeding season (spring-fall) than in the winter (McMillan and Irschick, 2010). The "credit-card hypothesis" suggests that individuals in urban populations will on average be less competitive than rural populations even if populations are denser because resources tend to be more readily available in urban habitats, easing selective for competitiveness (e.g., Hasegawa et al., 2014); in this case, however, it appears that the patchy distribution of preferred green anole habitat in the artificially-managed, lizard-dense TU location (Bloch and Irschick, 2006) forced adult males into close proximity with each other, resulting in unusually intense male-male competition.

Despite the apparently lower predation intensity at the TU locality, expansion into urban environments (or, alternatively, encroachment of urban habitat into natural species distributions) can nonetheless bring species into contact with novel pathogens and parasites or otherwise increase the risk of infection. This appears to have also occurred in the urban TU green anole population. Irschick et al. (2006a) documented infection in this population of green anoles by *Lepidodexia blakeae*, a sarcophagid fly. The fly larviposits on the skin, with the larvae developing inside the lizard until emerging from a wound and pupating in sediment. The open wounds in the lateral abdominal areas caused by the larvae during and immediately following active infection are large, and lizards that survive infection bear obvious scars. Irschick et al. (2006a) surveyed both the GHF and TU populations for incidences of *L. blakeae* infection over a 10-month period, and found no cases of either active infection or of scars in the GHF population. Urban TU lizards, however, exhibited infection rates ranging from 6.2% in the winter, to 7.6% the subsequent fall. However, the risk of infection was not distributed evenly across age/sex classes, with adult male green anole males being between 5 and 8 times more likely to be parasitized than juveniles or adult females (Irschick et al., 2006a). Despite reports elsewhere of as many as 17 larvae infesting a single green anole (Dodge, 1955), infections in the TU lizards are not always lethal, with 9.5 and 4.3% of sampled adult males bearing parasite scars in the spring and fall, respectively, of 2004 (Irschick et al., 2006a).

Previous studies have shown that the intensity of parasitism or predation can influence sexual selection by altering the conspicuousness of visual or auditory sexual displays (Zuk and Kolluru, 1998; Godin and McDonough, 2003; Zuk et al., 2006). Although the role of behavior, and display behavior in particular, in mediating parasite infection probability in green anoles is unknown, one possibility is that the overall high display rate of males in this population, coupled with the high male density (Bloch and Irschick, 2006), decreased wariness (Irschick et al., 2005a), and openness of the patchy TU green anole habitat collectively contributed to high male conspicuousness at the TU location, and thus increased male vulnerability to parasites. Green anole males with larger dewlaps also display more frequently (Johnson et al., 2011), which likely contributes further to their conspicuousness, as might the openness of the TU habitat; for example, Stroud et al. (2019) found that *A. sagrei* lizards in open urban environments displayed twice as frequently as those in natural environments. In addition to behavior increasing the risk of infection or parasitism, infection status might also alter behavior. For instance, *Anolis brevirostris* lizards heavily parasitized by ectoparasitic mites exhibited duller dewlaps and less frequent displays than individuals with fewer parasites (Cook et al., 2013). However, arguing against the conspicuousness hypothesis is the observation that active sarcophagid infections in the TU green anole population were observed only in the winter (Irschick et al., 2006a), when males are less likely to display. Indeed, individual dewlaps in TU lizards also change size over the course of a year, shrinking during the non-breeding season (Irschick et al., 2006b) due to reduced frequency of use in the fall and winter (Lailvaux et al., 2015).

Regardless of the mechanism, the main finding that the urban green anole population suffers a higher rate of infection than natural populations is consistent with results both from other *Anolis* species and from other lizards. Thawley et al. (2019) found that *A. sagrei* lizards from urban populations experienced higher intensity of parasite infection compared to conspecifics sampled from natural habitats (although they also found no effect of urbanization on infection intensity in another species, *A. cristatellus*). Furthermore, Lazíc et al. (2017) reported more variable but on average significantly higher blood parasite loads in urban versus rural populations of *Podarcis muralis* lizards. Higher rates of parasitism in urban populations might be driven by several factors, ranging from increased infection transmission at higher population densities (Cressler et al., 2016) to increased immune costs suffered by urban populations compared to natural populations. Artificial or dim light at night, for instance, can disrupt circadian rhythms, increasing susceptibility to infections and altering disease transmission dynamics (Kernbach et al., 2018). Thus far there have been no studies comparing the immune capacity of urban and rural populations of green anoles, although Husak and Lailvaux (2019) found that immunocompetence as assessed by phytohemagglutinin (PHA) challenge was not a significant predictor of mortality in an introduced and manipulated urban *A. carolinensis* population elsewhere in New Orleans. The seasonality of immune defenses in green anoles is also understudied (Tylan and Langkilde, 2017), and it may be that investment in immune defenses has a seasonal component as in other lizard species (e.g., Huyghe et al., 2010; see also Reedy et al., 2015).

Finally, It is also of note that the immune defenses of successful invaders tend to render them less susceptible to pathogens than natives (Lee et al., 2005); for example, invasive anoles were found to exhibit lower frequencies of malarial infection than native species in central Florida (Doan et al., 2019). Consequently, asymmetric immune strategies between green anoles and potential competitors, such as *A. sagrei*, could also affect green anole behavior, if only indirectly.

Population Structure and Demography

Population biology and demography are fundamental to evolutionary ecology. The number, age, and sex of animals in a given population can have consequences for behavior, life-history, and reproductive strategies. For example, operational sex ratio significantly influences the strength of sexual selection in animals, either through changes in mate choice or by affecting the strength of intrasexual competition (Janicke and Morrow, 2018). Male-biased sex ratios and resulting increased sexual competition can also lead to increased investment in body mass (Jarman, 1983), which can be achieved through adjustments in other key life history traits. Indeed, juvenile crickets that are exposed to increased numbers of adult male calls may adjust their development time such that they mature later than would otherwise be the case but at a larger body size (Kasumovic, 2013). Adult density effects on juveniles also exist in anoles; for example, *A. sagrei* juveniles alter their structural habitat use when adult male density is high

(Delaney and Warner, 2017), which could have implications for development trajectories given the documented morphological plasticity in this species (Losos et al., 2000; Bonneaud et al., 2016). It is currently unclear how the documented higher densities of organisms in urban environments affect either their population structures and sex ratios or, in turn, other aspects of their life-history, particularly for small, cryptic species such as green anoles.

Green anoles are considered model organisms for ecology and evolution (Lovern et al., 2004), and consequently several studies have considered the population ecology of free-ranging anoles in nature. However, the structure of *A. carolinensis* populations in urban areas have received relatively little attention. Work on Caribbean anoles in particular offers several testable predictions regarding how urban green anole populations might be affected by population size and density in particular. For example, Schoener and Schoener (1980) found that sex ratios and population densities differed among populations with different habitat types in four species of Bahamian anoles. Muralidhar and Johnson (2017) reported similar intraspecific variation in sex ratio in some species of Caribbean anoles. Furthermore, Schoener and Schoener (1980) also present a model predicting that numbers of females should vary more than numbers of males within populations over time, such that denser populations should have greater numbers of females.

Few studies have attempted to test these predictions among populations of green anoles, and the long-term demographic data required to do so are seldom collected. Michael (1972) used mark-recapture methods to study an urban population of 181 green anoles in eastern Texas from October 1966 through to May of 1970 but focused primarily on measuring growth rates. A similar multi-year study was conducted from February 1979 to July 1980 by Ruby (1984) in Metairie, an urban residential area outside of New Orleans. This study neither estimated population density nor broke down the age/sex structure by year, but it did specifically note a stable 1:1 sex ratio over the study period (Ruby, 1984). However, given that sex ratios may also cycle over time (Uller et al., 2007), the possibility exists that a longer study period could show dynamic sex ratios.

TEMPORAL PATTERNS OF SEX RATIO AND DENSITY IN WASHINGTON SQUARE PARK GREEN ANOLES

As an additional test of the above intra-population predictions, and to provide data as a reference for future studies of urban green anole populations, I analyze and present here the results of a 5-year mark-recapture study of an urban *A. carolinensis* population located in Washington Square Park (hereafter WSP) in the Faubourg Marigny neighborhood of downtown New Orleans, LA (N29.965005°, W90.057302°). This park, one hectare in area, is bordered by an iron fence and fringed with *A. elatior* palmetto plants which serve as the primary green anole habitat (as in the TU population; Irschick et al., 2005a). Other potential habitat includes man-made structures such as benches, trash cans, and playground equipment, as well as oak trees (*Quercus virginiana*) and small bushes of various species. Although lizards have at times been seen to use all of this habitat, the vast majority of anoles are observed on the palmetto plants and the fence. This park was chosen because it is entirely surrounded by roadway on all sides, and thus comprises a discrete population with likely minimal immigration and emigration. However, the areas immediately surrounding the park were also searched during each sampling period.

Methods

The WSP population was exhaustively censused twice per year over a 5-year period from 2010 to 2014 using methods consistent with Irschick et al. (2005a,b). Briefly, lizards were captured by hand or by noose and marked permanently and uniquely with visual implant elastomer (VIE) tags (Northwest Marine Technology, Inc., Shaw Island, WA, United States) on the ventral side of the limb elements. Lizards were sexed, weighed, and measured to the nearest 0.01 mm with Rok digital calipers (Rok International Industry Co., Limited, Shenzhen, China). Following Irschick et al. (2005b) I considered adult males to be greater than 45 mm snout-vent length (SVL), and adult females to be greater than 40 mm SVL. Upon capture the GPS coordinates were recorded and point of capture marked with colored tape. The next morning the lizards were released at the exact location from where they were collected. Prior to release each lizard was marked with a permanent marker just above the dorsal tail base to prevent recapture within the same sampling period; this marking is eliminated when the lizard next molts. Sampling occurred in the spring (April–May) and fall (September–October) of each year, at approximately the beginning and the end of the green anole breeding season, respectively.

Analyses

Following a recent study of sex ratios in anoles by Muralidhar and Johnson (2017) I calculated sex ratio as the proportion of males among all adults in the population. I calculated population density as density of adult lizards (lizards/m^2), and as densities of each sex/age class. I used a time-series analysis to test for autocorrelation in sex ratios and densities over the 5-year period. Densities varied markedly across seasons and years, which could also affect sex ratios. To test whether numbers of males and females varied differently over each season while controlling for effects of population density, I used a generalized linear model with Poisson errors with season, sex, and an interaction between season and sex as factors and population density as a covariate. To test whether numbers of males and females changed across seasons along with density, I fit a second such model with season, sex, density, and an interaction between sex and density as factors. I did this both to avoid uninterpretable three-way interactions, and to prevent overfitting any one model. I identified the minimum adequate models for each using log-likelihood ratio tests. I do not conduct any across-population analyses on density or sex ratio data because the GHF and TU data represent snapshots of single seasons

TABLE 1 | Best-fit models describing variation in number of lizards at the WSP population.

	Model term	Coefficient	SE
Number of lizards	Intercept	2.824	0.345
	Density (lizards/m^2)	217	64.587
	Season (Fall 2010)	0.024	0.167
	Season (Spring, 2011)	−0.357	0.315
	Season (Fall, 2011)	−0.088	0.228
	Season (Spring, 2012)	−0.0162	0.18
	Season (Fall, 2012)	−0.383	0.298
	Season (Spring, 2013)	0.006	0.164
	Season (Fall, 2013)	−1.2	0.423
	Season (Spring, 2014)	−0.011	0.188
	Season (Fall, 2014)	−0.013	0.157
	Sex (male)	−0.309	0.184
	Density:Sex (male)	61.208	31.74

The minimum adequate model for the first test of season:sex and the second test of density:sex reduce to the same model, with main effects of density and season. However, because the density:sex interaction was only marginally non-significant (see main text), I present the results of the model with the interaction. The reported coefficients give estimated change in the dependent variable between the baseline category and the category named in the table. The baseline category for Season is Season (Spring, 2010) and for Sex is Sex (Female).

whereas the WSP data comprises multiple seasons over 5 years, and choosing any specific season for comparison would be subjective. I used R version 3.6.0 (R Core Team, 2019) for all analyses.

RESULTS AND DISCUSSION

Sex ratios in WSP were close to 1:1 over the 5-year period, but where biased were almost always female-biased. Sex ratios showed no evidence of cycling over the 5-year period (Ljung-Box $\chi^2 = 0.456$, d.f. = 1, $P < 0.5$). Similarly, overall population density ($\chi^2 = 1$, d.f. = 1, $P < 0.312$) and densities of males ($\chi^2 = 0.132$, d.f. = 1, $P < 0.716$) and females ($\chi^2 = 2.65$, d.f. = 1, $P < 0.104$) were not autocorrelated among seasons.

The model for number of lizards retained season and density as factors, but sex and the interaction between sex and season were not significant. Thus, numbers of males and females do not change relative to each other once population density is accounted for. In the second model, the interaction between density and sex for number of animals was insignificant, but only marginally so (model with interaction compared to model without interaction: d.f. = 8, deviance = −3.723, $P < 0.054$). This interaction indicates larger numbers of males at higher population densities. Because these two models end up being identical with the exception of the marginal density:sex interaction, I present only the results of the second model with that interaction in **Table 1**.

Both **Figure 1** and the coefficients in **Table 1** indicate a clear reduction in population size in Fall, 2013. The reasons for this bottleneck are not immediately apparent; there were no changes in habitat nor any extreme weather events in 2013 that might account for any increased mortality. Nonetheless, the population recovered in the following sampling period (Spring, 2014) which is suggestive of some immigration, although hatchlings often appear late in the year as well.

The prediction that numbers of females should be more variable than that of males as population density changes was not supported in this case, as changes in density appear to be related to number of males in the population instead (**Table 1**). Schoener and Schoener (1980) specifically note that the phenomenon of female variability relating to density should be apparent in good habitats. Given that urban habitats differ in so many ways from those of natural populations,

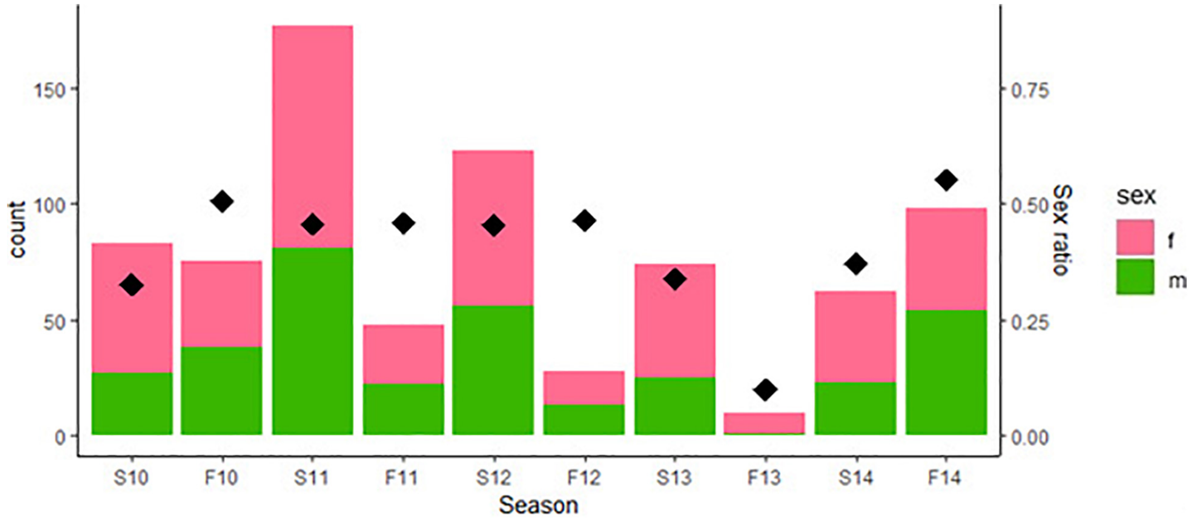

FIGURE 1 | Counts of adult male and adult female green anole lizards in the Washington Square Park population from 2010 to 2014 broken down by census period [i.e., by spring (S) and Fall (F) of each year]. Thus "S10" denotes the spring of 2010, "F10" the fall of 2010, and so on. Diamonds represent the sex ratio, calculated as proportion of males among all adults in the population as indicated on the right axis, for each census period.

one possible explanation for this discrepancy is that urban habitats are inferior to those inhabited by natural populations for this species.

CONCLUSION AND FUTURE DIRECTIONS

Urban populations show distinct differences in morphology, performance, and behavior in a number of animal taxa. This brief review demonstrates that *A. carolinensis* is among those species whose behavior and ecology are altered by urban environments. Drawing inferences from population comparisons is not without potential pitfalls, and indeed, Mayr (1963) claimed that "every population of a species differs from all others." Consequently, several of the differences noted here between urban and rural populations could be due not to effects of urbanization itself, but to any of the other myriad factors contributing to intraspecific and interpopulational variation. For example, a rigorous population comparison of green anole infestation by *L. blakea* should take into account the population ecology of the fly as well, and it may be that the higher infection rates in the TU population compared to the GHP population are more a function of local density effects on *L. blakea* as opposed to an urbanization effect on *A. carolinensis*. Indeed, the WSP population study I described above found only one active *L. blakea* infection and four individuals with parasite scars over a 5-year period despite WSP also being an urban population, indicating variation among urban populations in infection rate, mortality rate, or both. Previous studies have also indicated variation among green anole populations in such key traits as display type structure (Lovern et al., 1999) and dewlap color (Michaud and Echternacht, 1995).

Such caveats notwithstanding, these comparisons recapitulate several findings that characterize general differences between urban and rural populations in other animal species, and are thus likely to constitute real consequences of the urban habitat. Green anoles inhabiting urban environments are shaped differently; live at higher densities; are less wary; display more frequently; are more likely to suffer interference competition from invasive species; and appear to experience lower predation and higher intrasexual competition than conspecifics in natural populations. Other differences, such as disparate immune strategies or propensity for risk taking, are less supportable and suffer mainly from a lack of relevant data. In fact, a major message of this review is not how much is known about urban populations of green anoles, but rather how little is known regarding how green anoles have adapted to the urban environments which they appear to have inhabited for some time. This is particularly true for some aspects of population ecology, which have received less attention in urban populations of green anoles as compared to many Caribbean congenerics. The data presented here suggest tentatively that the temporal dynamics of populations in an urban environment could differ from those in natural habitats, although further tests in replicate populations are required before this conclusion can be reached.

Although this lack of data represents a challenge for the current paper, for the field of urban ecology it is instead an opportunity. Green anoles not only exhibit a large and environmentally heterogeneous distribution, they are also highly variable in morphology (Jaffe et al., 2016) and show substantial life-history variation across their North American range (Michaud and Echternacht, 1995). Indeed, the effects of urbanization on life-history have arguably not received the attention that they deserve, even though urban environments certainly hold the potential to affect animal life-histories (Ditchkoff et al., 2006). For example, birds appear to trade-off reproduction against survival in urban populations, exhibiting longer life spans but lower clutch sizes in urban environments and thereby adopting a slower life-history strategy compared to natural populations (Sepp et al., 2018), and underground populations of *Culex pipiens* mosquitoes in urban areas exhibit divergent life-cycles to aboveground populations (Byrne and Nichols, 1999; Asgharian et al., 2015). In this respect, green anoles represent an untapped resource for understanding how urbanization affects life-histories in small vertebrates given both their presence across the United States in urban environments and the variation in green anole life-history strategies across that same range. Yet another aspect of green anole urban ecology that has received less attention than it might, especially with regard to behavior, is thermal ecology. Temperature has been shown to impose selection on the green anole phenotype in the southern part of their range (Campbell-Staton et al., 2017), and there is evidence of selection on genes related to metabolism and behavior in the northern part of their range as well (Bourgeois and Boissinot, 2019). The combination of urban heat island effects (Campbell-Staton et al., 2020) with potential shifts in behavioral strategies at higher latitudes could facilitate the expansion of green anoles into urban areas in the northern extreme of the green anole range as the climate continues to warm. However, few data are currently available on the thermal preferences, tolerances, and performance curves of urban green anoles (but see Lailvaux and Irschick, 2007 for an example, again from an urban population in New Orleans), and there are potential costs to urban heat island effects that might mitigate any such benefits in reptiles (e.g., Hall and Warner, 2018).

Despite these opportunities, studies of urban populations also have shortcomings. Because patches of habitat that might harbor animal species in urban areas are often carefully managed, changes in management practice can also alter habitat structure or resource availability in such a way that overall habitat quality can be reduced. It is worth noting that the TU green anole population to which I have referred time and time again in this paper for all intents and purposes no longer exists; much of the palmetto habitat in the transect area was removed several years ago by the Tulane University groundskeepers, and that change in the physical environment, coupled with the growing numbers of *A. sagrei* for whom the new physical landscape is less of a deterrent, has made TU green anoles scarcer and more difficult to locate ever since. Thus, maintaining long-term study sites in urban areas can be problematic if the priorities of stakeholders - who may have less of an interest in biology than do urban ecologists - change. It is perhaps ironic that the same human activity that drives rampant urbanization can also render urban populations of certain animal species ephemeral.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusion of this article will be made available by the author, without undue reservation.

ETHICS STATEMENT

This animal study was reviewed and approved by the University of New Orleans Institutional Animal Care and Use Committee [IACUC protocol (UNO-11-004)].

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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REFERENCES

Ackley, J. W., Angilletta, M. J., DeNardo, D., Wu, B. S. J., and Wu, J. G. (2015). Urban heat island mitigation strategies and lizard thermal ecology: landscaping can quadruple potential activity time in an arid city. *Urban Ecosyst*.18, 1447–1459. doi: 10.1007/s11252-015-0460-x

Arnold, S. J. (1983). Morphology, performance, and fitness. *Am. Zool*.23, 347–361. doi: 10.1093/icb/23.2.347

Asgharian, H., Chang, P. L., Lysenkov, S., Scobeyeva, V. A., Reisen, W. K., and Nuzhdin, S. V. (2015). Evolutionary genomics of *Culex pipiens*: global and lcoal adaptations associated with climate, life-history traits and anthropogenic factors. *Proc. R. Soc. B Biol. Sci*.282:20150728. doi: 10.1098/rspb.2015.0728

Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W., and Ketterson, E. D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behav. Ecol*.23, 960–969. doi: 10.1093/beheco/ars059

Auer, S. K., Dick, C. A., Metcalfe, N. B., and Reznick, D. N. (2018). Metabolic rate evolves rapidly and in parallel with the pace of life history. *Nat. Commun*.9:6.

Avilés-Rodríguez, K. J., and Kolbe, J. J. (2019). Escape in the city: urbanization alters the escape behavior of *Anolis* lizards. *Urban Ecosyst*.22, 733–742. doi: 10.1007/s11252-019-00845-x

Barker, N. K. S., and Mennill, D. J. (2009). Song perch height in Rufous-and-White Wrens: does behaviour enhance efective communication in a tropical forest? *Ethology* 115, 897–904. doi: 10.1111/j.1439-0310.2009.01674.x

Bateman, P. W., and Fleming, P. A. (2009). To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. *J. Zool*.277, 1–14. doi: 10.1111/j.1469-7998.2008.00484.x

Battles, A. C., Moniz, M., and Kolbe, J. J. (2018). Living in the big city: preference for broad substrates results in niche expansion for urban Anolis lizards. *Urban Ecosyst*.21, 1087–1095. doi: 10.1007/s11252-018-0787-1

Battles, A. C., Whittle, T. K., Stehle, C. M., and Johnson, M. A. (2013). Effects of human land use on prey availability and body condition in the green anole lizard, *Anolis carolinensis*. *Herpetol. Conserv. Biol*.8, 16–26.

Bennett, A. F. and Huey, R. B. (1990). "Studying the evolution of physiological performance," *Oxford Surveys in Evolutionary Biology*, eds D. J. Futuyma and J. Antonovics (Oxford: Oxford University Press), 251-284.

Blair, R. B. (2001). "Birds and butterflies along urban gradients in two ecoregions of the United States: is urbanization creating a homogeneous fauna?," in *Bioltic Homogenization*, eds J. L. Lockwood and M. L. McKinney (Boston, MA: Springer).

Bloch, N., and Irschick, D. J. (2006). An analysis of inter-population divergence in visual display behavior of the green anole lizard (Anolis carolinensis). *Ethology* 112, 370–378. doi: 10.1111/j.1439-0310.2006.01162.x

Blumstein, D. T. (2014). "Attention, habituation, and anti-predator behaviour: implications for urban birds," in *Avian Urban Ecology* eds D. Gil and H. Brumm (Oxford: Oxford University Press), 41-53.

Blumstein, D. T., Fernández-Juricic, E., Zollner, P. A., and Garity, S. C. (2005). Inter-specific variation in avian responses to human disturbance. *J. Appl. Ecol*.42, 943–953. doi: 10.1111/j.1365-2664.2005.01071.x

Bonneaud, C., Marnocha, E., Herrel, A., Vanhooydonck, B., Irschick, D. J., and Smith, T. B. (2016). Developmental plasticity affects sexual size dimorphism in an anole lizard. *Funct. Ecol*.30, 235–243. doi: 10.1111/1365-2435.12468

Bourgeois, Y., and Boissinot, S. (2019). Selection at behavioural, developmental and metabolic genes is associated with the northward expansion of a successful tropical colonizer. *Mol. Ecol*.28, 3523–3543. doi: 10.1111/mec.15162

Byrne, K., and Nichols, R. A. (1999). Culex pipiens populations in London Underground tunnels: differentiation between surface and subterranean populations. *Heredity* 82, 7–15. doi: 10.1038/sj.hdy.6884120

Calsbeek, R., and Marnocha, E. (2006). Context dependent territory defense: the importance of habitat structure in *Anolis sagrei*. *Ethology* 112, 537–543. doi: 10.1111/j.1439-0310.2006.01194.x

Campbell-Staton, S. C., Cheviron, Z. A., Rochette, N. C., Catchen, J., Losos, J. B., and Edwards, S. V. (2017). Winter storms drive rapid phenotypic, regulatory, and genomic shifts in the green anole lizard. *Science* 357, 495–498. doi: 10.1126/science.aam5512

Campbell-Staton, S. C., Winchell, K. M., Rochette, N. C., Fredette, J., Maayan, I., Schweizer, R. M., et al. (2020). Parallel selection on thermal physiology facilitates repeated adaptation of city lizards to urban heat islands. *Nat. Ecol. Evol*. 4, 652-658.

Chejanovski, Z. A., Aviles-Rodriguez, K. J., Lapiedra, O., Preisser, E. L. and Kolbe, J. J. (2017). An experimental evaluation of foraging decisions in urban and natural forest populations of *Anolis lizards*. *Urban Ecosyst*. 20, 1011–1018. doi: /10.1007/s11252-017-0654-5

Cook, E. G., Murphy, T. G., and Johnson, M. A. (2013). Colorful displays signal male quality in a tropical anole lizard. *Naturwissenschaften* 100, 993–996. doi: 10.1007/s00114-013-1095-5

Cooke, A. S. (1980). Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. *Biol. Conserv*.18, 85–88. doi: 10.1016/0006-3207(80)90072-5

Cooper, W. E. (2015a). "Reptiles. Escaping From Predators," in *An Integrative View of Escape Decisions* eds W. E. Cooper and D. T. Blumstein (Cambridge: Cambridge University Press).

Cooper, W. E. (2015b). "Theory: models of escape behavior and resource use," in *Escaping From Predators: An Integrative View of Escape Decisions* eds W. E. Cooper and D.T. Blumstein (Cambridge: Cambridge University Press).

Cressler, C. E., Mcleod, D. V., Rozins, C., Van Den Hoogen, J., and Day, T. (2016). The adaptive evolution of virulence: a review of theoretical predictions and empirical tests. *Parasitology* 143, 915–930. doi: 10.1017/s003118201500092x

Damas-Moreira, I., Riley, J. L., Harrias, D. J., and Whiting, M. J. (2019). Can behaviour explain invasion success? A comparison between sympatric invasive and native lizards. *Anim. Behav*.151, 195–202. doi: 10.1016/j.anbehav.2019.03.008

Delaney, D. M., and Warner, D. A. (2017). Adult male density influences juvenile microhabitat use in a territorial lizard. *Ethology* 123, 157–167. doi: 10.1111/eth.12586

Delaney, K. S., Riley, S. P. D., and Fisher, R. N. (2010). A rapid, strong, and convergent genetic response to urban habitat fragmentation in four divergent and widespread vertebrates. *PLoS One* 5:e12767. doi: 10.1371/journal.pone.0012767.t001

Dill, A. K., Sanger, T. J., Battles, A. C., and Johnson, M. A. (2013). Sexual dimorphisms in habitat-specific morphology and behavior in the green anole lizard. *J. Zool*.290, 135–142. doi: 10.1111/jzo.12020

Ditchkoff, S. S., Saalfield, S. T., and Gibson, C. J. (2006). Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosyst*.9, 5–12. doi: 10.1007/s11252-006-3262-3

Doan, T. M., Devlin, B. G., and Greene, K. C. (2019). Malaria infection is lower in invasive anoles than aative anoles in Central Florida, USA. *J. Herpetol*.53, 22–26. doi: 10.1670/18-056

Dodge, H. R. (1955). Sarcophagid flies parasitic on reptiles. *Proc. Entomol. Soc. Washington* 57, 183-187.

Donihue, C. M., Herrel, A., Fabre, A. C., Kamath, A., Geneva, A. J., Schoener, T. W., et al. (2018). Hurricane-induced selection on the morphology of an island lizard. *Nature* 560:88. doi: 10.1038/s41586-018-0352-3

Edwards, J. R., and Lailvaux, S. P. (2012). Display behavior and habitat use in single and mixed populations of *Anolis carolinensis* and *Anolis sagrei* lizards. *Ethology* 118, 494–502. doi: 10.1111/j.1439-0310.2012.02037.x

Edwards, J. R., and Lailvaux, S. P. (2013). Do interspecific interactions between females drive shifts in habitat use? A test using the lizards *Anolis carolinensis* and *A. sagrei*. *Biol. J. Linn. Soc*.110, 843–851. doi: 10.1111/bij.12180

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *Am. Nat*.139, S125-S153.

Evans, J., Boudreau, K., and Hyman, J. (2010). Behavioural syndromes in urban and rural populations of song sparrows. *Ethology* 116, 588-595.

Fernández-Juricic, E., Poston, R., De Collibus, K., Morgan, T., Bastain, B., Martin, C., et al. (2005). Microhabitat selection and singing behavior patterns of male house finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the western U.S. *Urban Habit*.3, 49–69.

Fleishman, L. J. (1992). The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat*.139, S36-S61.

Fletcher, D. E., Hopkins, W. A., Standora, M. M., Arribas, C., Baionna-Parikh, J. A., Saldaña, T., et al. (2008). "Geckos as indicators of urban pollution," in *Urban Herpetology* eds J. C. Mitchell, R. E. J. Brown and B. Bartholomew (Humlebæk: Socoety for the Study of Amphibians and Reptiles).

Forman, R. T. (2014). *Urban Ecology: Science of Cities*. Cambridge: Cambridge University Press.

Garland, T., and Losos, J. B. (1994). "Ecological morphology of locomotor performance in squamate reptiles," in *Ecological Morphology: Integrative Organismal Biology,* eds P.C. Wainwright and S. Reilly (Chicago, CL: University of Chicago Press), 240-302.

Gilman, C. A., Bartlett, M. D., Gillis, G. B., and Irschick, D. J. (2012). Total recoil: perch compliance alters jumping performance and kinematics in green anole lizards (*Anolis carolinensis*). *J. Exp. Biol*.215, 220–226. doi: 10.1242/jeb.061838

Gilman, C. A., and Irschick, D. J. (2013). Foils of flexion: the effects of perch compliance on lizard locomotion and perch choice in the wild. *Funct. Ecol*.27, 374–381. doi: 10.1111/1365-2435.12063

Glor, R. E., Losos, J. B., and Larson, A. (2005). Out of Cuba: overwater dispersal and speciation among lizards in the Anolis carolinensis subgroup. *Mol. Ecol*.14, 2419–2432. doi: 10.1111/j.1365-294x.2005.02550.x

Godin, J. G. J., and McDonough, H. E. (2003). Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behav. Ecol*.14, 194–200. doi: 10.1093/beheco/14.2.194

Hall, J. M., and Warner, D. A. (2018). Thermal spikes from the urban heat island increase mortality and alter physiology of lizard embryos. *J. Exp. Biol*.221:jeb181552. doi: 10.1242/jeb.181552

Hall, J. W., and Warner, D. A. (2017). Body size and reproduction of a non-native lizard are enhanced in an urban environment. *Biol. J. Linn. Soc*.122, 860–871. doi: 10.1093/biolinnean/blx109

Hasegawa, M., Ligon, R. A., Giraudeau, M., Watanabe, M., and McGraw, K. J. (2014). Urban and colorful male house finches are less aggressive. *Behav. Ecol*.25, 641–649. doi: 10.1093/beheco/aru034

Hertz, P. E., Huey, R. B., and Nevo, E. (1982). Fight versus flight - body temperature influences defensive responses of lizards. *Anim. Behav*.30, 676–679. doi: 10.1016/s0003-3472(82)80137-1

Huey, R. B., Hertz, P. E., and Sinervo, B. (2003). Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat*.161, 357–366. doi: 10.1086/346135

Hurtado, G., and Mabry, K. E. (2017). Aggression and boldness in Merriam's kangaroo rat: an urban-tolerant species? *J. Mammol*. 98, 410–418. doi: 10.1093/jmammal/gyw199

Husak, J. F., and Lailvaux, S. P. (2019). Experimentally enhanced performance decreases survival in nature. *Biol. Lett*.15:20190160. doi: 10.1098/rsbl.2019.0160

Huyghe, K., Van Oystaeyen, A., Pasmans, F., Tadiæ, Z., Vanhooydonck, B., and Van Damme, R. (2010). Seasonal changes in parasite load and a cellular immune response in a colour polymorphic lizard. *Oecologia* 163, 867–874. doi: 10.1007/s00442-010-1646-9

Irschick, D. J., Carlisle, E., Elstrott, J., Ramos, M., Buckley, C. R., Vanhooydonck, B., et al. (2005a). A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biol. J. Linn. Soc*.85, 223–234. doi: 10.1111/j.1095-8312.2005.00487.x

Irschick, D. J., Gentry, G., Herrel, A., and Vanhooydonck, B. (2006a). Effects of sarcophagid fly infestations on green anole lizards (*Anolis carolinensis*): an analysis across seasons and age/sex classes. *J. Herpetol*.40, 107–112. doi: 10.1670/132-05a.1

Irschick, D. J., and Losos, J. B. (1999). Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. *Am. Nat.* 154, 298–305.

Irschick, D. J., Ramos, M., Buckley, C., Elstrott, J., Carlisle, E., Lailvaux, S. P., et al. (2006b). Are morphology-performance relationships invariant across different seasons? A test with the green anole lizard (*Anolis carolinensis*). *Oikos* 114, 49–59. doi: 10.1111/j.2006.0030-1299.14698.x

Irschick, D. J., Vanhooydonck, B., Herrel, A., and Meyers, J. J. (2005b). Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. *Biol. J. Linn. Soc*.85, 211–221. doi: 10.1111/j.1095-8312.2005.00486.x

Itescu, Y., Schwartz, R., Meiri, S., and Pafillis, P. (2017). Intraspecific competition, not predation, drives lizard tail loss on islands. *J. Anim. Ecol*.86, 66–74. doi: 10.1111/1365-2656.12591

Jaffe, A. L., Campbell-Staton, S. C., and Losos, J. B. (2016). Geographical variation in morphology and its environmental correlates in a widespread North American lizard, Anolis carolinensis (Squamata: Dactyloidae). *Biol. J. Linn. Soc*.117, 760–774. doi: 10.1111/bij.12711

Janicke, T., and Morrow, E. H. (2018). Operational sex ratio predicts the opportunity and direction of sexual selection across animals. *Ecol. Lett*.21, 384–391. doi: 10.1111/ele.12907

Jarman, P. (1983). Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biol. Rev.* 58, 485–520. doi: 10.1111/j.1469-185X.1983.tb00398.x

Johnson, M. A., Cohen, R. E., Vandecar, J. R., and Wade, J. (2011). Relationships among reproductive morphology, behavior, and testosterone in a natural population of green anole lizards. *Physiol. Behav*.104, 437–445. doi: 10.1016/j.physbeh.2011.05.004

Johnson, M. A., Kirby, R., Wang, S., and Losos, J. B. (2006). What drives variation in habitat use by *Anolis* lizards: habitat availability or selectivity? *Can. J. Zool*. 84, 877–886. doi: 10.1139/z06-068

Johnson, M. T. J., and Munshi-South, J. (2017). Evolution of life in urban environments. *Science* 358:eaam8327. doi: 10.1126/science.aam8327

Kasumovic, M. M. (2013). The multidimensional consequences of the juvenile environment: towards an integrative view of the adult phenotype. *Anim. Behav*.85, 1049–1059. doi: 10.1016/j.anbehav.2013.02.009

Kern, E. M. A., and Langerhans, R. B. (2019). Urbanization alters swimming performance of a stream fish. *Front. Ecol. Evol*.6:12. doi: 10.3389/fevo.2018.00229

Kernbach, M. E., Hall, R. J., Burkett-Cadena, N. D., Unnasch, T. R., and MArtinf, L. B. (2018). Dim light at night: physiological effects and ecological consequences for infectious disease. *Integr. Comp. Biol*.58, 995–1007.

Kolbe, J. J., Battles, A. C., and Aviles-Rodriguez, K. J. (2016). City slickers: poor performance does not deter Anolis lizards from using artificial substrates in human-modified habitats. *Funct. Ecol*.30, 1418–1429.

Kolbe, J. J., and Losos, J. B. (2005). Hind-limb length plasticity in *Anolis carolinensis*. *J. Herpetol*.39, 674–678. doi: 10.1670/87-05n.1

Kuo, C. Y., Irschick, D. J., and Lailvaux, S. P. (2015). Trait compensation between boldness and the propensity for tail autotomy under different food availabilities in similarly aged brown anole lizards. *Funct. Ecol*.29, 385–392. doi: 10.1111/1365-2435.12324

Lailvaux, S. P., Alexander, G. J., and Whiting, M. J. (2003). Sex-based differences and similarities in locomotor performance, thermal preferences, and escape behaviour in the lizard *Platysaurus intermedius wilhelmi*. *Physiol. Biochem. Zool*.76, 511–521. doi: 10.1086/376423

Lailvaux, S. P., Cespedes, A. M., and Houslay, T. M. (2019). Conflict, compensation, and plasticity: sex-specific, individual-level trade-offs in green anole (*Anolis carolinenis*) performance. *J. Exp. Zool. A* 331, 280-289.

Lailvaux, S. P., and Irschick, D. J. (2006). A functional perspective on sexual selection: insights and future prospects. *Anim. Behav*.72, 263–273. doi: 10.1016/j.anbehav.2006.02.003

Lailvaux, S. P., and Irschick, D. J. (2007). Effects of temperature and sex on jump performance and biomechanics in the lizard *Anolis carolinensis*. *Funct. Ecol*.21, 534–543. doi: 10.1111/j.1365-2435.2007.01263.x

Lailvaux, S. P., Leifer, J., Kircher, B. K., and Johnson, M. A. (2015). The incredible shrinking dewlap: signal size, skin elasticity, and mechanical design in the green anole lizard (Anolis carolinensis). *Ecol. Evol*.5, 4400–4409. doi: 10.1002/ece3.1690

Langerhans, R. B., and DeWitt, T. J. (2004). Shared and unique features of evolutionary diversification. *Am. Nat*.164, 335–349. doi: 10.1086/422857

Lapiedra, O. (2018). Urban behavioral ecology: lessons from *Anolis* lizards. *Integr. Comp. Biol*.58, 939–947.

Lapiedra, O., Schoener, T. W., Leal, M., Losos, J. B., and Kolbe, J. J. (2018). Predator-driven natural selection on risk-taking behavior in anole lizards. *Science*,360:1017. doi: 10.1126/science.aap9289

Lazíc, M. M., Carretero, M. A., Živkovíc, U., and Crnobrnja-Isailovíc, J. (2017). City life has fitness costs: reduced body condition and increased parasite load in urban common wall lizards, *Podarcis muralis*. *Salamandra* 53, 10–17.

Lazic, M. M., Kaliontzopoulou, A., Carretero, M. A., and Crnobrnja-Isailovic, J. (2013). Lizards from urban areas are more asymmetric: using fluctuating asymmetry to evaluate environmental disturbance. *PLos One* 8:e84190. doi: 10.1371/journal.pone.0084190

Lee, K. A., Martin, L. B., and Wikelski, M. C. (2005). Responding to inflammatory challenges is less costly for a successful avian invader, the house sparrow (*Passer domesticus*), than its less-invasive congener. *Oecologia*. 143, 243-250.

Liu, Z., He, C., and Wu, J. (2016). The relationship between habitat loss and fragmentation during urbanization: an empirical evaluation from 16 world cities. *PLoS One*. 11:e0154613. doi: 10.1371/journal.pone.0154613

Losos, J. B. (2011). Convergence, adaptation, and constraint. *Evolution* 65, 1827–1840. doi: 10.1111/j.1558-5646.2011.01289.x

Losos, J. B., Creer, D. A., Glossip, D., Goellner, R., Hampton, A., Roberts, G., et al. (2000). Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution* 54, 301–305. doi: 10.1554/0014-3820(2000)054[0301:eioppi]2.0.co;2

Lovern, M., and Jenssen, T. A. (2003). Form emergence and fixation of head bobbing displays in the green anole lizard (*Anolis carolinensis*): a reptilian model of signal ontogeny. *J. Comp. Physiol*.117, 133–141. doi: 10.1037/0735-7036.117.2.133

Lovern, M. B., Holmes, M. M., and Wade, J. (2004). The green anole (*Anolis carolinensis*): a reptilian model for laboratory studies of reproductive morphology and behavior. *ILAR J*.45, 54–64. doi: 10.1093/ilar.45.1.54

Lovern, M. B., Jenssen, T. A., Orrell, K. S., and Tuckak, T. (1999). Comparisons of temporal display structure across contexts and populations in male *Anolis carolinensis:* signal stability or lability? *Herpetologica* 55, 222–234.

Lowry, H., Lill, A., and Wong, B. B. M. (2013). Behavioural responses of wildlife to urban habitats. *Biol. Rev*.88, 537–549. doi: 10.1111/brv.12012

Luther, D. A., Phillips, J., and Derryberry, E. P. (2016). Not so sexy in the city: urban birds adjust songs to noise but compromise voval performance. *Behav. Ecol*.27, 332–340. doi: 10.1093/beheco/arv162

Markovchick-Nicholls, L., Regan, H. M., Deutschman, D. H., Widyanata, A., Martin, B., Noreke, L., et al. (2008). Relationships between human disturbance and wildlife land use in urban habitat fragments. *Conserv. Biol*.22, 99–109. doi: 10.1111/j.1523-1739.2007.00846.x

Marnocha, E., Pollinger, J., and Smith, T. B. (2011). Human-induced morphological shifts in an island lizard. *Evol. Appl*.4, 388–396. doi: 10.1111/j.1752-4571.2010.00170.x

Martin, J., and López, P. (1995). Influence of habitat structure on the escape tactics of the lizard *Psammodromus algirus*. *Can. J. Zool*.73, 129–132. doi: 10.1139/z95-014

Mayr, E. (1963). *Animal Species and Evolution*. Cambridge, MA: Harvard University Press.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biol. Conserv*.127, 247–260. doi: 10.1016/j.biocon.2005.09.005

McMillan, D. M., and Irschick, D. J. (2010). Experimental test of predation and competition pressures on the green anole (*Anolis carolinensis*) in varying structural habitats. *Journal of Herpetology*,44, 272–278. doi: 10.1670/08-196.1

Michael, E. D. (1972). Growth rates in *Anolis carolinensis*. *Copeia* 1972, 575–577. doi: 10.2307/1442932

Michaud, E. J., and Echternacht, A. C. (1995). Geographic variation in the life history of the lizard *Anolis carolinensis* and support for the pelvic constraint model. *J. Herpetol*.29, 86–97. doi: 10.2307/1565090

Mikula, P. (2014). Pedestrian density influences flight distances of urban birds. *ARDEA* 102, 53–60. doi: 10.5253/078.102.0105

Moore, M. P., Riesch, R., and Martin, R. A. (2016). The predictability and magnitude of life-history divergence to ecological agents of selection: a meta-analysis in livebearing fishes. *Ecol. Lett*.19, 435–442. doi: 10.1111/ele.12576

Munoz, M. M., and Losos, J. B. (2018). Thermoregulatory behavior simultaneously promotes and forestalls evolution in a tropical lizard. *Am. Nat*.191, E15-E26.

Muralidhar, P., and Johnson, M. A. (2017). Sexual selection and sex ratios in *Anolis* lizards. *J. Zool*.302, 178–183. doi: 10.1111/jzo.12446

Orrell, K. S., and Jenssen, T. A. (2003). Heterosexual signalling by the lizard *Anolis carolinensis*, with intersexual comparisons across contexts. *Behaviour* 140, 603–634. doi: 10.1163/156853903322149469

Parris, K. M., Velik-Lord, M., and North, J. M. A. (2009). Frogs call at a higher pitch in traffic noise. *Ecol. Soc*.14:25.

Petren, K., and Case, T. J. (1998). Habitat structure determines competition intensity and invasion success in gecko lizards. *Proc. Natl. Acad. Sci. U.S.A.* 95, 11739–11744. doi: 10.1073/pnas.95.20.11739

Putnam, B. J., Pauly, G. P., and Blumstein, D. T. (2020). Urban invaders are not bold risk-takers: a study of 3 invasive lizards in Southern California. *Curr. Zool.* doi: 10.1093/cz/zoaa015

Reedy, A. M., Cox, C. L., Chung, A. K., Evans, W. J., and Cox, R. M. (2015). Both sexes suffer increased parasitism and reduced energy storage as costs of reproduction in the brown anole. *Anolis sagrei*. *Biol. J. Linn. Soc*.117, 516–527. doi: 10.1111/bij.12685

Reznick, D. A., Bryga, H., and Endler, J. A. (1990). Experimentally induced life-history evolution in a natural population. *Nature* 346, 357–359. doi: 10.1038/346357a0

Rhodes, M., and Catterall, C. (2008). Spatial foraging behavior and use of an urban landscape by a fast-flying bat, the Molossid *Tadarida australis*. *J. Mammal*.89, 34–42. doi: 10.1644/06-mamm-a-393.1

Ruby, D. E. (1984). Male breeding success and differential access to females in *Anolis carolinensis*. *Herpetologica* 40, 272–280.

Scales, J., Hyman, J., and Hughes, M. (2011). Behavioral syndromes break down in urban song sparrow populations. *Ethology* 117, 887–895. doi: 10.1111/j.1439-0310.2011.01943.x

Schoener, T., and Schoener, A. (1980). Densities, sex rations, and population structure in four species of Bahamian *Anolis* lizards. *J. Anim. Ecol.*49, 19–53. doi: 10.2307/4276

Sepp, T., McGraw, K. J., Kaasik, A., and Giraudeau, M. (2018). A review of urban impacts on avian life-history evolution: does city living lead to a slower pace-of life? *Glob. Change Biol.* 24, 1452–1469. doi: 10.1111/gcb.13969

Slabbekoorn, H., and Peet, M. (2003). Birds sing at higher pitch in urban noise. *Nature* 424:267. doi: 10.1038/424267a

Sol, D., Lapiedra, O., and González-Lagos, C. (2013). Behavioral adjustments for a life in the city. *Anim. Behav.*85, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Sol, D., Maspons, J., Gonzalez-Voyer, A., Morales-Castilla, I., Garamszegi, L. Z., and Møller, A. P. (2018). Risk-taking behavior, urbanization, and the pace of life in birds. *Behav. Ecol. Sociobiol.* 72. doi: 10.1007/s00265-018-2463-0

Stroud, J. T., Colom, M., Ferrer, P., Palermo, N., Vargas, V., Cavallini, M., et al. (2019). Behavioral shifts with urbanization may facilitate biological invasion of a widespread lizard. *Urban Ecosyst.* 22, 425–434. doi: 10.1007/s11252-019-0831-9

R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Thawley, C. J., Moniz, H. A., Merritt, A. J., Battles, A. C., Michaelides, S. N., and Kolbe, J. J. (2019). Urbanization affects body size and parasitism but not thermal preferences in *Anolis* lizards. *J. Urban Ecol.*5, 1–9.

Tylan, C., and Langkilde, T. (2017). Local and systemic immune responses to different types of phytohemagglutanin in the green anole: lessons for field ecoimmunologists. *J. Exp. Zool. Part A Ecol. Integr. Physiol.*327, 322–332. doi: 10.1002/jez.2108

Tyler, R. K., Winchell, K. M., and Revell, L. J. (2016). Tails of the city: caudal autotomy in the tropical lizard, *Anolis cristatellus*, in urban and natural areas of Puerto Rico. *J. Herpetol.*50, 435–441. doi: 10.1670/15-039

Uller, T., Pen, I., Wapstra, E., Beukeboom, L. W., and Komdeur, J. (2007). The evolution of sex ratios and sex-determining systems. *Trends Ecol. Evol.*22, 292–297. doi: 10.1016/j.tree.2007.03.008

Vanhooydonck, B., Herrel, A., and Irschick, D. J. (2007). Determinants of sexual differences in escape behavior in lizards of the genus *Anolis*: a comparative approach. *Integr. Comp. Biol.*47, 200–210. doi: 10.1093/icb/icm018

Vervust, B., Lailvaux, S. P., Grbac, I., and Van Damme, R. (2008). Do morphological condition indices predict locomotor performance in the lizard *Podarcis sicula*? *Acta Oecol.* 34, 244–251. doi: 10.1016/j.actao.2008.05.012

Watling, J. I., and Donnelly, M. A. (2006). Fragments as islands: a synthesis of faunal responses to habitat patchiness. *Conserv. Biol.*20, 1016–1025. doi: 10.1111/j.1523-1739.2006.00482.x

Winchell, K. M., Briggs, D., and Revell, L. J. (2019). The perils of city life: patterns of injury and fluctuating asymmetry in urban lizards. *Biol. J. Linn. Soc.*126, 276–288. doi: 10.1093/biolinnean/bly205

Winchell, K. M., Carlen, E. J., Puente-Rolón, A. R., and Revell, L. J. (2018a). Divergent habitat use of two urban lizard species. *Ecol. Evol.*2018, 25–35. doi: 10.1002/ece3.3600

Winchell, K. M., Maayan, I., Fredette, J. R., and Revell, L. J. (2018b). Linking locomotor performance to morphological shifts in urban lizards. *Proc. R. Soc. B Biol. Sci.*285:10.

Winchell, K. M., Reynolds, R. G., Prado-Irwin, S. R., Puente-Rolon, A. R., and Revell, L. J. (2016). Phenotypic shifts in urban areas in the tropical lizard *Anolis cristatellus*. *Evolution* 70, 1009–1022. doi: 10.1111/evo.12925

Woolbright, L. L., Hara, A. H., Jacobsen, C. M., Mautz, W. M., and Benevides, F. L. (2006). Population densities of the coqui, *Eleutherodactylus coqui* (Anura: Leptodactylidae) in newly invaded Hawaii and in native Puerto Rico. *J. Herpetol.* 40, 122–126. doi: 10.1670/79-05w.1

Ydenberg, R. C., and Dill, L. M. (1986). The economics of fleeing from predators. *Adv. Stud. Anim. Behav.*16, 229–249. doi: 10.1016/s0065-3454(08)60192-8

Zozaya, S. M., Alford, R. A., and Schwarzkopf, L. (2015). Invasive house geckos are more willing to use artificial lights than are native geckos. *Austr. Ecol.*40, 982–987. doi: 10.1111/aec.12287

Zuk, M., and Kolluru, G. R. (1998). Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol.*73, 415–443. doi: 10.1086/420412

Zuk, M., Rotenberry, J. T., and Tinghitella, R. M. (2006). Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biol. Lett.*2, 521–524. doi: 10.1098/rsbl.2006.0539

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Does Use of Backyard Resources Explain the Abundance of Urban Wildlife?

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While urbanization is clearly contributing to biodiversity loss, certain wildlife assemblages can paradoxically be diverse and abundant in moderately developed areas. One hypothesis to explain this phenomenon is that abundant anthropogenic resources for wildlife (i.e., food and shelter) outweigh the costs associated with urbanization. To test this hypothesis, we used camera traps to measure mammal species richness, diversity, and relative abundance (i.e., detection rate) in 58 residential yards in Raleigh, North Carolina, focusing on six types of features that might be used as resources: animal feeding, vegetable gardens, compost piles, chicken coops, brushpiles, and water sources. We also placed cameras at random control sites within each yard and sampled forests in nearby suburban and rural areas for comparison. We fit mixed-effects Poisson models to determine whether yard features, yard-scale characteristics, or landscape-scale landcover predicted mammal relative abundance for eight species. We also tested if the relative abundance of native canid predators in yards was related to the number of prey (rodents and lagomorphs). Species richness, diversity, and relative abundance of most mammal species was higher in yards and suburban forests than in rural forests. Within a yard, purposeful feeding had the strongest effect on animal relative abundance, with eastern gray squirrels (*Sciurus carolinensis*) being the most common (32.3 squirrels/day at feeders; 0.55 at control sites; 0.29 in suburban forests; and 0.10 in rural forests). We observed species using (e.g., eating) most yard features, although canids were less likely than other taxa to use resources in yards. The presence of a yard feature did not strongly affect the abundance of species at the control site in the yard, suggesting the influence of these features was highly localized. The relative abundance of predators had a positive association with prey relative abundance, and predators were less common in yards with fences. These results demonstrate that there is high use of anthropogenic resources, especially supplemental feeding by urban wildlife, and this increase in prey species may then attract predators, which supports the hypothesis that use of supplemental food resources explains the abundance of urban wildlife.

Keywords: camera trap, mammal, relative abundance, species richness, supplemental feeding

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INTRODUCTION

Urbanization is increasing globally, with 55% of the world's population currently living in urban areas, 68% projected to live in urban areas in the year 2050 (United Nations et al., 2017), and urban land use expanding 9,687 km^2 per year between 1985 and 2015 (Liu et al., 2020). Urban areas are often viewed as being biodiversity deserts, largely due to the negative impacts of urbanization on the environment (McKinney, 2006; Mcdonald et al., 2008), including land-use and land-cover change (Foley et al., 2005), altered biogeochemical cycles, increased CO_2 emissions driving climate change, and changes in wildlife abundance, distribution, and community composition (Grimm et al., 2008).

While urbanization is clearly contributing to biodiversity loss, certain wildlife assemblages, sometimes including sensitive and threatened species, are paradoxically found to be more diverse and abundant in moderately developed areas than in wild areas (e.g., Ives et al., 2016; Parsons et al., 2018). Even some large carnivores, often thought to avoid urban areas, have been found to exploit resources associated with urbanization (Bateman and Fleming, 2012). One explanation for the abundance of urban wildlife is that moderate levels of disturbance may result in a heterogeneous landscape that can support both good competitors and good colonizers (i.e., the intermediate disturbance hypothesis; Grime, 1973; Connell, 1978). Another explanation suggests that altered interspecific interactions among synanthropic and urbanophobic species may allow more species to thrive in urban areas (El-Sabaawi, 2018). For example, the decline of some apex predators in urban areas (e.g., Ordeñana et al., 2010) could reduce the contribution of top-down control in structuring ecological communities, thereby "releasing" mesopredators (Crooks and Soulé, 1999) and subsequently depressing prey species (e.g., rodents and lagomorphs). However, prey species are also often abundant in urban areas, resulting in a "predation paradox" that could be explained by the "human shield" hypothesis (Berger, 2007), where prey species exploit areas dominated by humans to avoid predators, or by the abundance of anthropogenic resources in urban areas, which provide food and shelter to wildlife in multiple trophic levels (Faeth et al., 2005; Rodewald et al., 2011; Fischer et al., 2012).

Urban areas house a diversity of resources for wildlife, including intentional food sources (e.g., feeders), unintentional food sources (e.g., gardens, compost piles, chicken coops), water, and shelter (e.g., brushpiles). These resources are often located in residential yards, which form a mosaic of small, independently managed green spaces throughout urban landscapes (Gaston et al., 2013). For example, it was estimated that over 47 million people spent approximately \$4.85 billion on birdseed and food for other wildlife in the United States in 2016 (U.S. Department of the Interior et al., 2018). Further, 35% of all households in the United States spent \$3.5 billion on vegetable gardening in 2013, with the number of participants increasing annually (National Gardening Association, 2014).

Wildlife use of urban resources has been extensively studied in the avian community (e.g., Cannon et al., 2005; Daniels and Kirkpatrick, 2006; Fuller et al., 2007; Goddard et al., 2010), but relatively little is known about how urban resources affect mammal communities. Reed and Bonter (2018) found that birdfeeders attracted eastern gray squirrels (*Sciurus carolinensis*) and northern raccoons (*Procyon lotor*), but they did not evaluate other yard features. Kays and Parsons (2014) evaluated mammal use of residential yards, but primarily focused on the effects of chicken coops, fences, and domestic dogs (*Canis familiaris*). A more comprehensive understanding of how the most common urban food and shelter resources affect mammal abundance in residential yards could help explain the abundance of urban wildlife and provide insight into the implications of backyard management on mammals, which could inform urban planning (Lepczyk et al., 2017). Our objective was to test the hypothesis that food and shelter resources in yards are an important factor explaining why some mammals are abundant in urban landscapes, in comparison with predation risk and landscape-scale attributes that are typically used to model animal distribution. Further, given concerns of predators [e.g., coyotes (*Canis latrans*)] being attracted to anthropogenic resources (Murray and St. Clair, 2017) or increased prey abundance (Prevedello et al., 2013), resulting in human-wildlife conflict (Soulsbury and White, 2015), an additional objective was to identify whether increasing prey abundance was related to an increase of predators in yards.

We hypothesized that resources in yards would influence the activity, distribution, and community structure of mammals in urban areas and that supplemental feeding (intentional and unintentional) would have the largest effect on the relative abundance of mammals (e.g., Boutin, 1990; Reed and Bonter, 2018). We predicted that increasing natural vegetation in the yard and in the surrounding landscape would also be associated with higher mammal relative abundances (Daniels and Kirkpatrick, 2006; Magle et al., 2009), but mammal relative abundance would be reduced in yards with fences or outdoor pets (Kays and Parsons, 2014). Finally, we predicted supplemental feeding would result in higher mammal abundance both locally (at the food source) and throughout the yard.

MATERIALS AND METHODS

Study Area

We conducted our study on residential yards and natural areas surrounding Raleigh and Durham, North Carolina (hereafter, Raleigh). The primary study area, including residential yards and suburban forests within ∼5 km radius of yards, was approximately 1,807 km^2 with an estimated human population of 1.14 million and a mean housing density of ∼534 houses/km^2. We also surveyed sites that occurred in forests with low housing density (<0.5 houses/km^2) within ∼130 km of yard sites ("rural" sites; **Figure 1**). Most of the primary study area was developed (∼54%), with

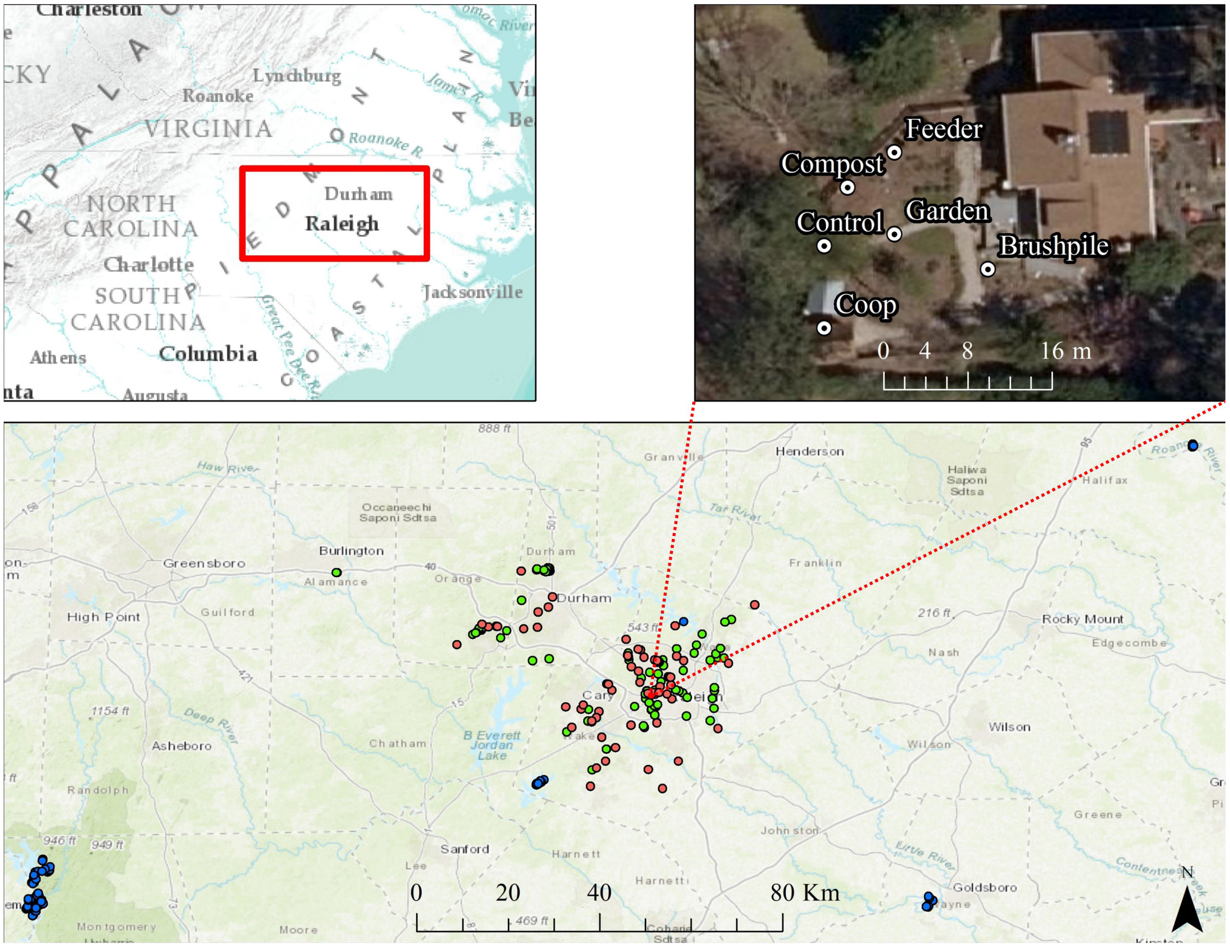

FIGURE 1 | Locations of residential yard (pink dots), suburban forest (green dots), and rural forest (blue dots) trail cameras surrounding Raleigh, North Carolina from 2012 to 2016. One representative yard is shown, with a camera placed at each feature in the yard (feeder, compost, chicken coop, garden, brushpile, and control site). Basemaps are Esri World Topographic and World Imagery maps.

forests (∼34%) and agricultural lands (∼4%) interspersed throughout the region.

Mammal Surveys

From March through October 2016, we set motion-triggered, low-glow infrared trail cameras (Reconyx Hyperfire PC 900; hereafter, "cameras") in 58 residential yards (hereafter, "yards"), spaced at least 100 m apart ($\bar{x} = 2.87$ km, range = 133 m–14.6 km), throughout the study area. We defined a yard as the portion of a residential parcel regularly maintained or managed (e.g., mowed, gardened, landscaped) by the homeowner, generally within approximately 100 m of the household. Approximately 88% of yards were spaced >500 m apart and 97% were spaced > 250 m apart. Given most species detected in our study have relatively small home ranges, particularly in urban environments, we were not concerned with spatial autocorrelation.

Housing density at yard sites averaged 378 houses/km^2. Most yards had at least one of six common yard features that may attract mammals, including bird or mammal feeders (n = 30), gardens (n = 31), compost (n = 29), chicken coops (n = 9), brushpiles (n = 39), or water features (n = 29). Two yards had none of these features. We set cameras approximately 0.5 m high, facing one of each unique feature types in the yard. We also set a camera at a random control site at least 3 m ($\bar{x} = 20$ m, range = 3–119 m) from the nearest feature in the yard (**Figure 1**). We set cameras to take a burst of 5 pictures at approximately 1 photo/second each time triggered, with no lag time between triggers, and left cameras for approximately 3 weeks ($\bar{x} \approx 21$ days), resulting in a total of 4,608 trap nights. We recorded other yard characteristics, including presence of fence, percent cover of trees within 100 m, percent of yard with natural vegetation, presence of domestic animals, and yard size. We also estimated landscape-scale attributes, including percent forest and housing development within 1 km of the yard using the United States National Landcover Dataset (Fry et al., 2011) and the Silvis housing density dataset (Hammer et al., 2004) in ArcMap (Version 10.1, ESRI, Redlands, California, United States).

As a comparison to yard sites, we also acquired data from cameras set from February–October 2012–2016 at random sites in "suburban" (147–1,000 houses/km^2; n = 105; trap nights = 2,277) and "rural" (<12.67 houses/km^2; n = 72; trap nights = 1,522) forests near Raleigh, NC (see Parsons et al., 2018). Suburban and rural forest cameras were set using the same methodology as yard sites, except cameras did not have a paired control site. Suburban forest sites averaged ∼305 houses/km^2 and rural forest sites averaged <1 house/km^2.

We uploaded photos from cameras into software[1] that groups photos taken <60 s apart into independent sequences. Using the software, we identified the number of unique individuals of each species in each sequence. We also identified whether a species was using the yard feature the camera was facing (e.g., eating the food source or climbing through the brushpile) or just passing by. Photo identifications were reviewed by an independent party to ensure accuracy in classification (McShea et al., 2016).

Analytical Methods

We used the iNEXT package (Hsieh et al., 2020) in R (R Core Development Team, 2019) to calculate species richness (effective number of species) and Shannon diversity (effective number of common species) of mammals, excluding mice and rats, at yard features and in suburban and rural forests. Specifically, we used incidence data from camera traps to calculate sample-size and coverage-based rarefaction/extrapolation curves and 95% confidence limits for Hill numbers (i.e., effective number of species) with diversity order $q = 0$ (species richness) and $q = 1$ (Shannon diversity; Chao et al., 2014; Hsieh et al., 2016).

We calculated mammal relative abundance (i.e., detection rate) by counting the number of each species detected on a camera in each sequence and dividing by the number of days the camera was active. Then, we calculated the mean and standard deviation of relative abundance, grouping by feature type and forest type (suburban or rural). We also calculated the proportion of sites in which the yard feature was used when a species was present.

We fit three sets of models to evaluate the influence of yard features on species-specific mammal relative abundance within yards. The first model evaluated how yard features influenced mammal relative abundance at the feature location, in relation to variables at larger scales. Using data from cameras next to yard features and control sites, we fit separate mixed-effects Poisson regression models for 8 of the most commonly detected species, including eastern gray squirrel, northern raccoon, Virginia opossum (*Didelphis virginiana*), white-tailed deer (*Odocoileus virginianus*), eastern cottontail (*Sylvilagus floridanus*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), and coyote. We included an extra error term in the model to account for overdispersion and included an "offset" term equivalent to the natural log of the number of days the camera was active. We included species-specific count as the response, and yard feature type, percent forest within 1 km, average housing density within 1 km, percent tree cover within 100 m, proportion of the yard with natural vegetation, presence of a fence surrounding the yard, presence of pets (domestic cats or dogs), and yard size as fixed effects in the model. We chose landscape variables (forest cover and housing density within 1 km) because previous studies in a similar region found these variables to be influential on mammal occupancy (Kays et al., 2017; Parsons et al., 2019). To account for unmodeled variation in mammal relative abundance among yards, we included yard identification as a random effect and estimated unique intercepts for each yard. We centered and scaled all continuous covariates. See **Supplementary Table 1** for a description of all model covariates.

The second model evaluated how the presence of a feature in yard influenced mammal relative abundance throughout the yard, beyond the feature. This model was also a Poisson regression model, but only included data from control cameras in yards and did not include a random effect. This model used species-specific count as a response, and included categorical variables identifying whether each feature was present in the yard. We also included all other yard and landscape attribute covariates that we included in the first model.

The final model evaluated how predator relative abundance in yards was related to prey relative abundance. This model was similar to the first, but we grouped species into a "predator" cohort (coyote, red fox, gray fox) and a "prey" cohort (eastern gray squirrel, eastern chipmunk, eastern cottontail, and mouse/rat species). We included predator count as the response and prey count, yard characteristics, and landscape attributes as predictors in the model to evaluate the relative contribution of each factor in predicting predator abundance in yards. We did not include yard feature variables in the model because there was high correlation between these variables and prey abundance.

We fit global models for each species within a Bayesian framework using the R2jags package (Su and Yajima, 2015) in R (R Core Development Team, 2019). We estimated posterior distributions of predictors by running 3 Markov Chain Monte Carlo (MCMC) chains, each for 1,000,000 iterations, with a burn-in of 250,000, and thinning of 10. We determined that predictors influenced the response if 95% credible intervals (between 2.5 and 97.5% quantiles) of parameter estimates did not overlap zero. We identified whether models converged by ensuring $\hat{R}$ values were <1.1 (Gelman and Rubin, 1992) and by examining posterior distributions and MCMC chains. We also used posterior predictive checks to calculate a Bayesian p-value (p_B) to assess model fit, assuming $0.1 < p_B < 0.9$ represented adequate fit (Gelman et al., 2014).

RESULTS

We detected 10, 13, and 9 wild mammal species on cameras in yards, suburban forests, and rural forests, respectively. Species richness and Shannon diversity did not vary considerably across yard features, but was generally lower in rural forests (**Figure 2**). Eleven wild species [white-tailed deer, eastern gray squirrel, northern raccoon, gray fox, eastern cottontail, red fox, coyote, woodchuck (*Marmota monax*), American beaver (*Castor canadensis*), eastern fox squirrel (*Sciurus niger*), and southern flying squirrel (*Glaucomys Volans*)] and

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[1] emammal.si.edu

mouse/rat species had higher relative abundances in suburban forests, compared to rural forests. Seven species [eastern gray squirrel, gray fox, Virginia opossum, eastern cottontail, red fox, woodchuck, and eastern chipmunk (*Tamias striatus*)] had higher relative abundances at control sites in yards, compared to suburban or rural forests. Bobcats (*Lynx rufus*) were detected most in rural forests and were never detected in yards (**Supplementary Table 2**).

White-tailed deer had the highest relative abundance in suburban ($\bar{x} = 1.27$/day; *SD* = 2.19) and rural ($\bar{x} = 1.03$/day; *SD* = 1.37) forests, while eastern gray squirrels had the highest relative abundance in yards (control site $\bar{x} = 0.55$/day; *SD* = 1.32). Feeders in yards attracted the most mammals, with eastern gray squirrels ($\bar{x} = 32.33$/day, *SD* = 40.92), northern raccoons ($\bar{x} = 1.86$/day, *SD* = 3.22), and eastern chipmunks ($\bar{x} = 1.47$/day, *SD* = 4.18) detected most frequently (**Figure 3** and **Supplementary Table 2**).

Overall, mammals used (e.g., ate or drank from, paused to examine, or took shelter in) 69% of the features where they were detected. Canids only used features at 53% of sites, while all other species used 71% of features. Eastern chipmunks used 85% of features where they were detected, while coyotes only used 33% of features. Mammals were most likely to use feeders (82% of sites) and gardens (77% of sites), but only used brushpiles at 56% of sites (**Supplementary Figure 1**).

All models converged and passed posterior predictive checks. The effect of yard feature type, yard characteristics, and landscape attributes on mammal relative abundance varied by species. Feeders had strong positive associations with the relative abundances of four species: eastern gray squirrel [β = 4.41, 95% credible interval (CI) = 3.68–5.18], eastern cottontail (β = 1.41, 95% CI = 0.39–2.46), northern raccoon (β = 2.37, 95% CI = 1.65–3.12), and Virginia opossum (β = 1.48, 95% CI = 0.57–2.41; **Figures 4**, **5**). Compost sites had positive associations with the relative abundances of northern raccoons (β = 1.70, 95% CI = 0.93–2.48) and Virginia opossums (β = 1.71, 95% CI = 0.82–2.63), but a negative association with the relative abundance of red foxes (β = −2.26, 95% CI = −4.83 to −0.10). Other yard characteristics and landscape features had less of an association with relative abundance of mammal species (**Figure 4**).

There were almost no effects of the presence of features in the yard on mammal relative abundances at the control site (**Figure 4**); although, coyotes were detected less in yards with water features (β = −13.60, 95% CI = −25.90 to −3.66). Yard-scale characteristics had more of an influence on mammal relative abundances at control sites. For example, red fox (β = −10.95, 95% CI = −24.33 to −1.33) and gray fox (β = −11.84, 95% CI = −25.37 to −1.62) had lower relative abundances in yards with full fences; northern raccoons (β = −2.55, 95% CI = −4.90 to −0.60) and Virginia opossums (β = −3.96, 95% CI = −9.30 to −0.22) had lower relative abundances in yards with pets; and eastern gray squirrels (β = −2.58, 95% CI = −4.93 to −0.68) and eastern cottontails (β = −3.93, 95% CI = −8.81 to −0.63) had lower relative abundances in larger yards. Landscape-scale characteristics also influenced some mammal detection rates in yards. White-tailed deer had higher relative abundances in yards with more forest within 1 km (β = 1.51, 95% CI = 0.08–3.20) and coyotes had higher relative abundances in yards with more housing development within 1 km (β = 4.56, 95% CI = 1.45–8.28), while eastern cottontails had lower relative abundance with more housing development (β = −10.95, 95% CI = −24.33 to −1.33; **Figure 4**).

The number of predators using yards had a small, but positive association with prey relative abundance (β = 0.28, 95% CI = 0.036–0.52). It would take prey count to increase by approximately 713 to double the number of predators in a yard. Predator relative abundance was lower in yards with full fences (β = −3.46, 95% CI = −5.79 to −1.48), but no other yard or landscape characteristics influenced predator relative abundance in yards (**Figure 5**).

DISCUSSION

A variety of mammals made use of either purposeful or incidental feeders (e.g., compost, gardens) in backyards, resulting in highly localized animal abundance, which we suggest helps explain the abundance of urban wildlife. Apart from a few exceptions, there was higher species richness/diversity and higher relative abundance of mammals in yards, compared to rural areas, and mammal detections increased substantially around supplemental feeders. Further, we frequently documented mammals eating anthropogenic food resources, demonstrating that mammal detections by feeders were related to feeding behavior and not coincidental. These results are consistent with other research related to supplemental feeding effects on mammal populations (e.g., Boutin, 1990; Sullivan, 1990; Bozek et al., 2007; Prevedello et al., 2013; Reed and Bonter, 2018), but are novel in that they also demonstrate the relative importance of supplemental feeding on urban mammal abundance, compared with factors such as other common yard features, landscape attributes, and predation risk.

Beyond supplemental food sources, other yard features were generally less associated with mammal relative abundance in our study. Most notably, there were few strong, positive associations between mammal detection rates and water sources, except for eastern gray squirrels and northern raccoons. Raleigh gets 7.6–11.4 cm precipitation per month on average (U.S. Climate Data, 2020), and there were many natural water sources in the surrounding area. Thus, mammals may not be water-limited in our study area and we expect there would be stronger associations between water sources and mammal abundance in more arid environments (e.g., McKee et al., 2015). Another notable observation was the low of use of brushpiles, except for eastern gray squirrels. Brushpiles are known to be important refugia for variety of taxa (e.g., Trent and Rongstad, 1974; Gorenzel et al., 1995; Bouget and Duelli, 2004; Sperry and Weatherhead, 2010), but the addition of brushpiles may not influence wildlife abundance or survival when they are not a limiting resource (e.g., Goguen et al., 2015). Further, urban wildlife will use anthropogenic structures for refugia (Lowry et al., 2013), so brushpiles or other natural refugia within yards may not be as important as they are in more natural areas. Finally, chicken coops were relatively unimportant drivers

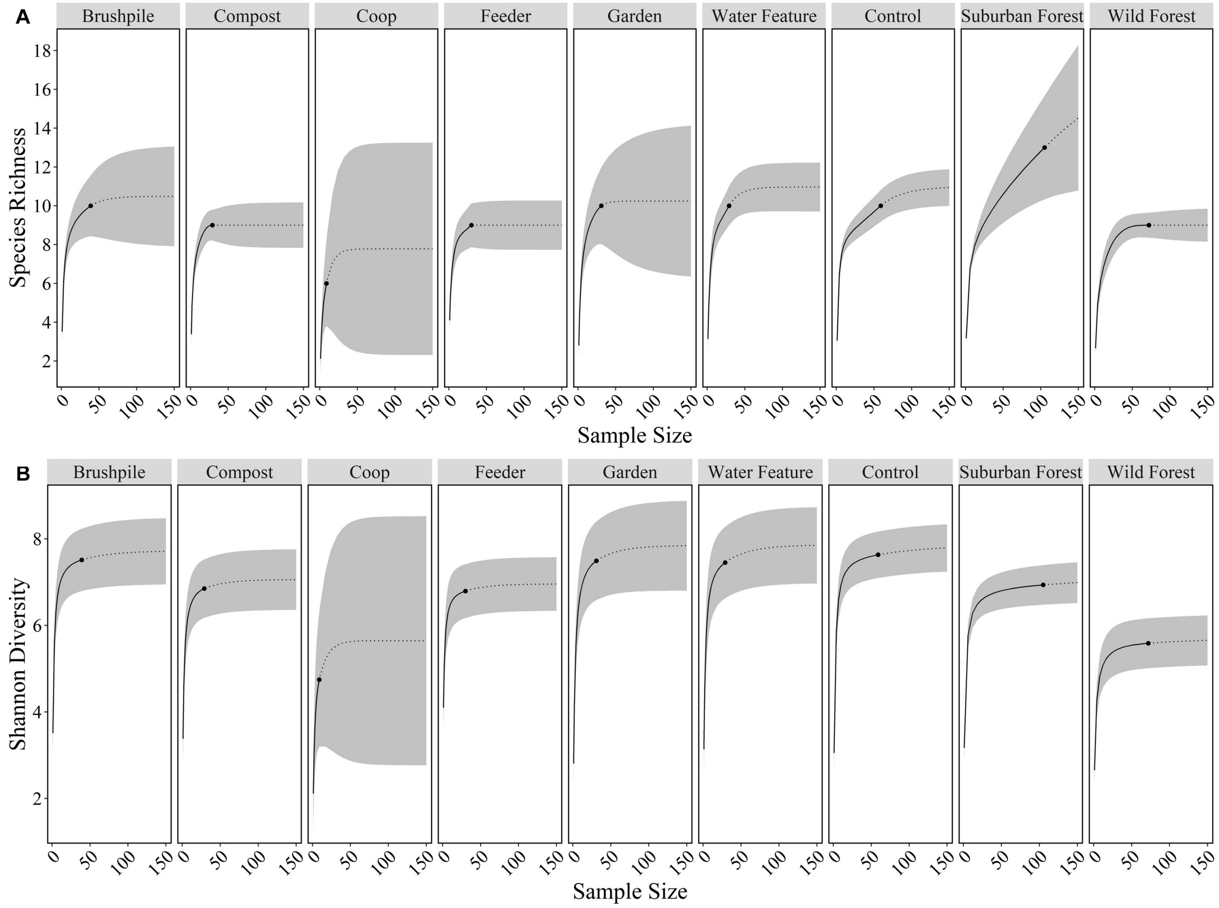

FIGURE 2 | Species richness **(A)** and Shannon diversity **(B)** of mammals at features in residential yards (brushpiles, compost piles, chicken coops, bird and mammal feeders, gardens, water features, control sites), suburban forests, and rural forests surrounding Raleigh, North Carolina from 2012 to 2016. Black dots are the observed species richness or diversity at a feature, solid lines are the interpolated values, dotted lines are the extrapolated values, and gray ribbons are the 95% confidence intervals across sample sizes.

of mammal relative abundance in our study; although, there was a 95 and 97% probability that coops had a positive influence on eastern gray squirrel and northern raccoon relative abundance, respectively. Kays and Parsons (2014) reported similar results, finding raccoons were the only mesopredator positively associated with chicken coops.

While resources in yards attracted rodents, lagomorphs, and some mesopredators, the activity of other mammals was more related to yard characteristics and landscape attributes. Yards with full fences generally had lower mammal relative abundance, with the strongest effects on gray fox, red fox, and Virginia opossums. The presence of domestic cats and dogs in the yard also negatively influenced mammal abundance, but only strongly affected northern raccoons and Virginia opossums. Kays and Parsons (2014) had similar findings, generally observing less mammal activity in fenced-in yards with dogs. These results are not surprising, as full fences will deter some mammals from entering a yard, and domestic animals are known to disturb wildlife (Lenth et al., 2008; Hughes and Macdonald, 2013; Loss et al., 2013). However, yards with supplemental feeders and fences/pets still attracted more mammals than fenceless/pet-free yards without feeding, particularly for species that could climb over or under fences (e.g., eastern gray squirrels, northern raccoons, eastern chipmunks), further supporting our finding that supplementary feeding drives mammal abundance in yards.

Mammal relative abundance in yards was least related to landscape attributes in our study. White-tailed deer were more likely to be detected in yards with more forest within 1 km of the yard, which is consistent with other research in the study area (Kays and Parsons, 2014). Most interestingly, coyotes detected in yards had positive associations with housing development within 1 km. Coyotes are increasingly being found in urban landscapes (e.g., Gehrt, 2004; Gehrt et al., 2009), and other research in the Raleigh area found coyotes in all development levels around the city (Parsons et al., 2018). We are unsure of the explanation for this result, but speculate coyotes using residential yards were part of a cohort that has become more adapted to urban landscapes. Thus, these coyotes were more likely to be detected within areas of greater housing development.

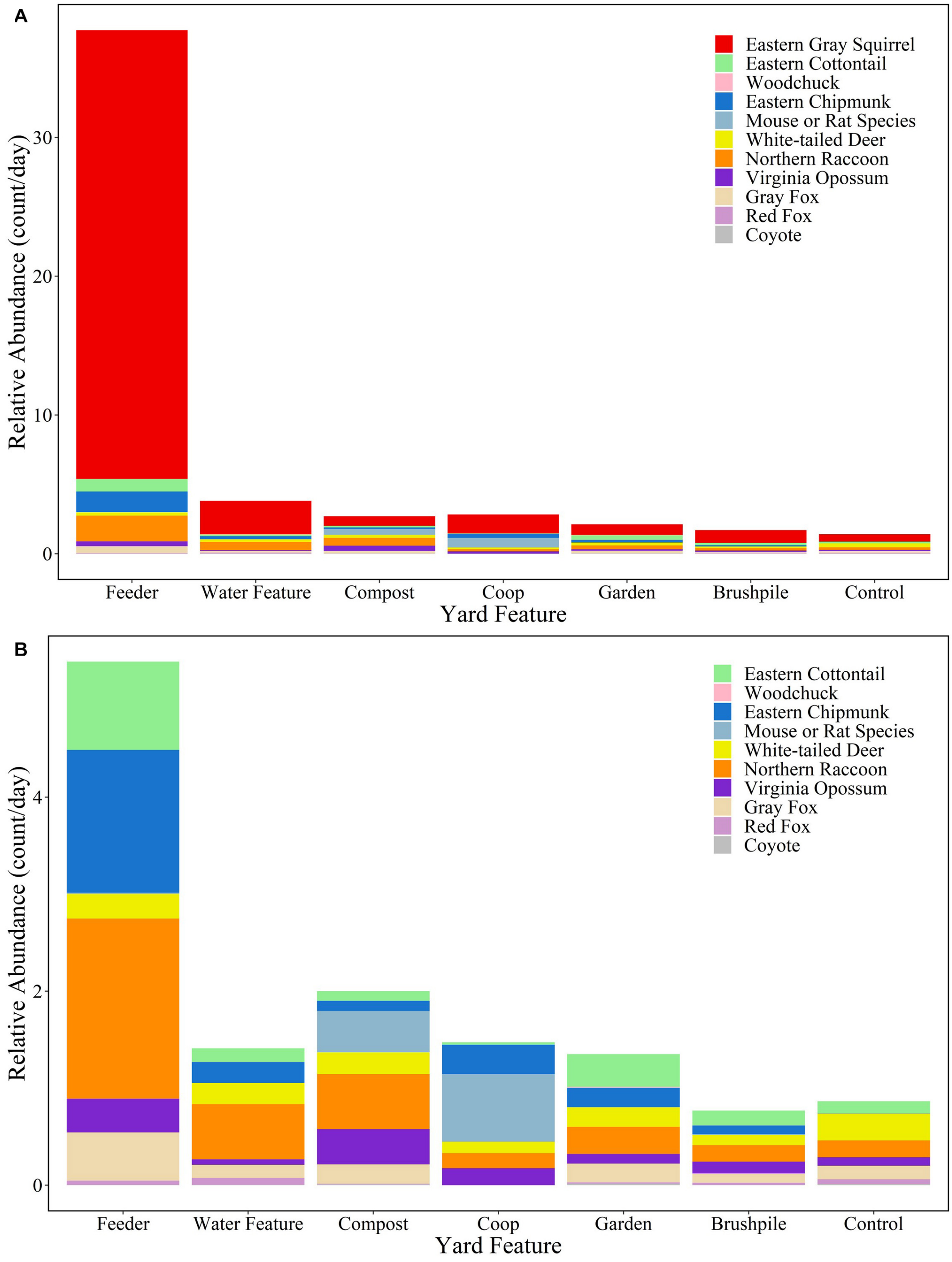

FIGURE 3 | Relative abundance (count/day) of mammal species at yard features in Raleigh, North Carolina in 2016. Figure **(A)** includes all species, while Figure **(B)** excludes eastern gray squirrels to highlight relative abundances of other species.

Top-down forces (i.e., predation) can play a large role in population fluctuations of species at lower trophic levels (e.g., Hairston et al., 1960) through density- or trait-mediated processes (Abrams et al., 1996); however, we did not find direct support for this hypothesis in our study. We detected most predators (i.e., native canids) more frequently in yards, compared to nearby rural areas, so the high abundance of prey in yards was not likely related to a reduction in predation risk, as predicted by the "human shield" hypothesis (Berger, 2007). Instead, we suggest that bottom-up forces from supplemental feeding are driving

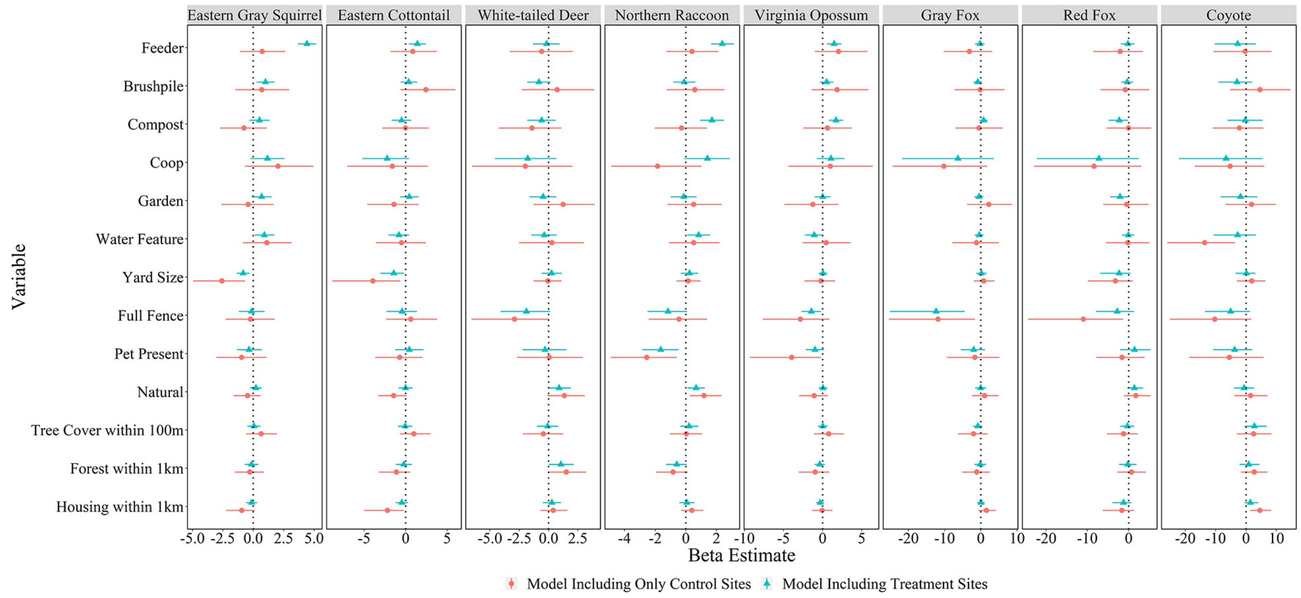

FIGURE 4 | Mean beta estimates (points) and 95% credible intervals (horizontal error bars) for variables explaining mammal relative abundances in residential yards in Raleigh, North Carolina in 2016. Feeders, brushpiles, compost, chicken coops, gardens, and water features represent local-level variables; yard size, full fence, pet present, natural (proportion of yard with natural vegetation), and tree cover within 100 m represent yard-scale variables; and proportion forest within 1 km and housing density within 1 km represent landscape-scale (i.e., neighborhood) variables. Blue markers represent models including treatment sites (cameras facing features) in yards and red markers represent models only including control sites in yards. Thus, feature variables included in control-only models represent whether the feature was present somewhere in the yard, while feature variables for treatment models represent cameras that faced the feature. Credible intervals that overlap the vertical dotted line (Beta = 0) represent variables without a strong influence on species-specific relative abundance.

increases in prey abundance, which may also have cascading effects through the mammal community, given the positive association between prey and predator relative abundance in yards. Prey abundance was the only factor with a positive association with predator abundance in yards; however, the effect was quite small, and predator abundance varied considerably, so we suspect predator abundance is being determined by additional, unmodeled factors.

Predator abundance in yards could also be related to direct consumption of supplemental food resources, although we did not find much support for this hypothesis in our study. Coyotes were found to select for yards with anthropogenic food, particularly compost, in Alberta (Murray and St. Clair, 2017) and coyotes may eat more anthropogenic resources when living in an urban-wild matrix (Newsome et al., 2015). Further, over half of the stomach contents of urban red foxes in Switzerland was anthropogenic (Contesse et al., 2004). We did not find strong positive associations between canid relative abundance and supplemental food features, but we did observe some of the species occasionally eating supplemental food. For example, we observed three coyotes and three red foxes by compost, but only one of each ate the compost. In contrast, we observed eight gray foxes by compost and each individual ate the compost. Individual differences in exploitation of anthropogenic food sources could be related to a variety of factors such as personality traits (i.e., boldness) or health status. For example, Murray and St. Clair (2017) found that coyotes with sarcoptic mange (*Sarcoptes scabiei*) were more likely to visit compost piles than healthy coyotes. A more focused study on interspecific interactions between predators and prey (e.g., Fischer et al., 2012), as well as predator demography, activity patterns, health, and diet selection in urban ecosystems would help elucidate the influence of anthropogenic resources on predator-prey relationships.

Past research suggests that the ecological implications of supplemental feeding are nuanced. There is evidence that supplemental feeding leads to reduced animal movements (Prange et al., 2003; Gehrt, 2004; Bozek et al., 2007; Gehrt et al., 2009) and may have positive effects on wildlife survival and reproductive rates (e.g., Adams et al., 2005; Bateman and Fleming, 2012). However, feeders could also act as an ecological trap for target species (e.g., birds) due to negative interspecific interactions with non-target species, such as squirrels (e.g., Reed and Bonter, 2018). For example, the hyperabundance of gray squirrels at supplemental feeding sites could interfere with avian use of feeders (Bonnington et al., 2014b) and result in reductions in avian species diversity and abundance for species that are susceptible to nest predation by squirrels (Bonnington et al., 2014a). Further, much of the positive demographic effects are realized in synanthropic species, which could outcompete non-synathropic species, thereby reducing community evenness and biodiversity in urban areas (Shochat et al., 2010). Mammal use of supplemental feeding sites could also have disease implications (Becker and Hall, 2014; Becker et al., 2015). We show that the

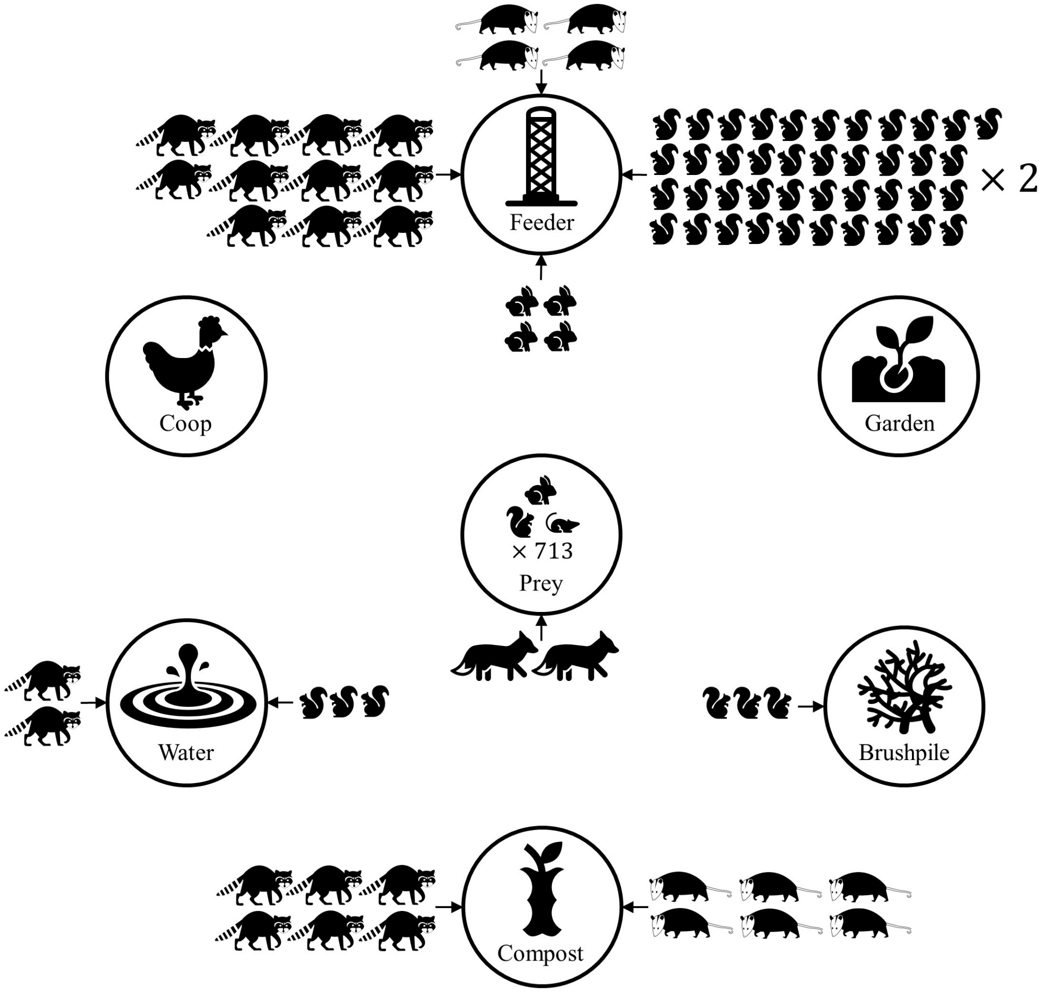

FIGURE 5 | Conceptual diagram demonstrating predicted mammal count at yard features, based on Poisson regression models of mammal count data from residential yards in Raleigh, North Carolina in 2016. Only strong associations between features and mammal count are shown. Eastern gray squirrels, eastern cottontails, northern raccoons, and Virginia opossums had higher relative abundance at some yard features, compared to control sites within a yard. Yards with higher prey (rodents and lagomorphs) relative abundance were more likely to have higher predator (wild canid) relative abundance. The number of mammal icons represents the relative risk ratio, compared to a control site in the yard. Thus, a yard feature with two raccoons suggests there are predicted to be twice as many raccoons at the feature, relative to the control site. The predicted number of predator detections doubled when prey detections increased by 713.

presence of a feature in a yard generally did not affect mammal abundance at the control site, regardless of high mammal abundance near the feature, suggesting mammal use of features in yards was highly localized. This aggregation of mammals could increase the probability of disease transmission among wildlife and from wildlife to humans (e.g., Soulsbury and White, 2015).

CONCLUSION

Overall, our study provides more evidence that moderately developed landscapes can contain a high diversity and abundance of mammals, sometimes higher than wild sites, which lends support to the intermediate disturbance hypothesis as an explanation for the abundance of urban wildlife. In the context of urban landscapes, a variety of factors could be considered "disturbance," including fragmentation of habitat, increased heterogeneity in habitat types, and introduction of supplemental food and structure resources. We found a large association between the relative abundance of some mammal species and supplemental food resources, which we posit is the primary explanation for the increase in species diversity and abundance in moderately developed areas. While predator-prey dynamics also likely influence urban mammal communities, we did not find strong support for this hypothesis in our study, other than a minor effect of prey species on predator relative abundance in residential yards. We also did not find strong support for an influence of landscape-scale factors on mammal relative abundance in yards; however, there are likely many other factors across spatial and temporal scales that we did not evaluate, such as landscape patchiness or connectivity, that could contribute to our findings.

Our findings only represent data surrounding one city in the United States. The effects of backyard resources on mammal relative abundance and community dynamics could vary across urban areas with different populations or urban structure. Thus, we caution extrapolation of our results and recommend further replication of our study across other urban sites. Further, we describe and discuss the ecological implications of abundant urban wildlife, but do not discuss the social implications, which are a crucial component of urban wildlife ecology, management, and conservation. For further information regarding the potential negative and positive implications of abundant urban wildlife and wildlife provisioning, we recommend reading reviews by Soulsbury and White (2015) and Cox and Gaston (2018).

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

Ethical review and approval was not required for the animal study because we used non-invasive techniques (trail cameras) to collect data related to mammal abundance.

AUTHOR CONTRIBUTIONS

CH analyzed the data and wrote the majority of the manuscript. AP and RK collected the data and helped develop and revise the manuscript. JM helped develop and revise 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.2020.570771/full#supplementary-material

REFERENCES

Abrams, P. A., Menge, B. A., Mittlebach, G. G., Spiller, D. A., and Yodzis, P. (1996). "The role of indirect effects in food webs," in *Food Webs: Integration of Patterns and Dynamics*, eds G. A. Polis and K. O. Winemiller (Boston, MA: Springer), 371–393.

Adams, L. W., VanDruff, L. W., and Luniak, M. (2005). "Managing urban habitats and wildlife," in *Techniques for Wildlife Investigations and Management*, ed. C. E. Braun (Lawrence, KS: Allen Press), 714–739.

Bateman, P. W., and Fleming, P. A. (2012). Big city life: carnivores in urban environments. *J. Zool.* 287, 1–23. doi: 10.1111/j.1469-7998.2011.00887.x

Becker, D. J., and Hall, R. J. (2014). Too much of a good thing: resource provisioning alters infectious disease dynamics in wildlife. *Biol. Lett.* 10:20140309. doi: 10.1098/rsbl.2014.0309

Becker, D. J., Streicker, D. G., Altizer, S., and Lafferty, K. (2015). Linking anthropogenic resources to wildlife–pathogen dynamics: a review and meta-analysis. *Ecol. Lett.* 18, 483–495. doi: 10.1111/ele.12428

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.* 3, 620–623. doi: 10.1098/rsbl.2007.0415

Bonnington, C., Gaston, K. J., and Evans, K. L. (2014a). Relative roles of grey squirrels, supplementary feeding, and habitat in shaping urban bird assemblages. *PLoS One* 9:e109397. doi: 10.1371/journal.pone.0109397

Bonnington, C., Gaston, K. J., Evans, K. L., and Downs, C. (2014b). Assessing the potential for Grey Squirrels *Sciurus carolinensis* to compete with birds at supplementary feeding stations. *Ibis* 156, 220–226. doi: 10.1111/ibi.12107

Bouget, C., and Duelli, P. (2004). The effects of windthrow on forest insect communities: a literature review. *Biol. Conserv.* 118, 281–299. doi: 10.1016/j.biocon.2003.09.009

Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Can. J. Zool.* 68, 203–220. doi: 10.1139/z90-031

Bozek, C., Prange, S., and Gehrt, S. (2007). The influence of anthropogenic resources on multi-scale habitat selection by raccoons. *Urban Ecosyst.* 10, 413–425. doi: 10.1007/s11252-007-0033-8

Cannon, A. R., Chamberlain, D. E., Toms, M. P., Hatchwell, B. J., and Gaston, K. J. (2005). Trends in the use of private gardens by wild birds in Great Britain 1995-2002. *J. Appl. Ecol.* 42, 659–671.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., et al. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84, 45–67. doi: 10.1890/13-0133.1

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310. doi: 10.1126/science.199.4335.1302

Contesse, P., Hegglin, D., Gloor, S., Bontadina, F., and Deplazes, P. (2004). The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mamm. Biol.* 69, 81–95.

Cox, D. T. C., and Gaston, K. J. (2018). Human–nature interactions and the consequences and drivers of provisioning wildlife. *Philos. T. R. Soc. B.* 373:20170092. doi: 10.1098/rstb.2017.0092

Crooks, K. R., and Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400, 563–566. doi: 10.1038/23028

Daniels, G. D., and Kirkpatrick, J. B. (2006). Does variation in garden characteristics influence the conservation of birds in suburbia? *Biol. Conserv.* 133, 326–335.

El-Sabaawi, R. (2018). Trophic structure in a rapidly urbanizing planet. *Funct. Ecol.* 32, 1718–1728. doi: 10.1111/1365-2435.13114

Faeth, S. H., Warren, P. S., Shochat, E., and Marussich, W. A. (2005). Trophic dynamics in urban communities. *Bioscience* 55, 399–407.

Fischer, J. D., Cleeton, S. H., Lyons, T. P., and Miller, J. R. (2012). Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *Bioscience* 62, 809–818. doi: 10.1525/bio.2012.62.9.6

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., et al. (2005). Global consequences of land use. *Science* 309, 570–574. doi: 10.1126/science.1111772

Fry, J. A., Xian, G., Jin, S. M., Dewitz, J. A., Homer, C. G., Yang, L. M., et al. (2011). Completion of the 2006 National Land Cover Database for the conterminous United States. *Photogramm. Eng. Rem. Sens.* 77, 858–864.

Fuller, R. A., Irvine, K. N., Devine-Wright, P., Warren, P. H., and Gaston, K. J. (2007). Psychological benefits of greenspace increase with biodiversity. *Biol. Lett.* 3, 390–394.

Gaston, K. J., Ávila-Jiménez, M. L., Edmondson, J. L., and Jones, J. (2013). REVIEW: managing urban ecosystems for goods and services. *J. Appl. Ecol.* 50, 830–840. doi: 10.1111/1365-2664.12087

Gehrt, S. D. (2004). "Ecology and management of striped skunks, raccoons, and coyotes in urban landscapes," in *Predators and People: From Conflict to Conservation*, eds N. Fascione, A. Delach, and M. Smith (Washington, DC: Island Press), 81–104.

Gehrt, S. D., Anchor, C., and White, L. A. (2009). Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *J. Mammal.* 90, 1045–1057. doi: 10.1644/08-MAMM-A-277.1

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., and Rubin, D. B. (2014). *Bayesian Data Analysis*, 3rd Edn. Boca Raton, FL: CRC Press.

Gelman, A., and Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Stat. Sci.* 7, 457–511.

Goddard, M. A., Dougill, A. J., and Benton, T. G. (2010). Scaling up from gardens: biodiversity conservation in urban environments. *Trends Ecol. Evol.* 25, 90–98. doi: 10.1016/j.tree.2009.07.016

Goguen, C. B., Fritsky, R. S., and Julian, G. J. S. (2015). Effects of brush piles on small mammal abundance and survival in Central Pennsylvania. *J. Fish Wildl. Manag.* 6, 392–404. doi: 10.3996/022015-JFWM-012

Gorenzel, P. W., Mastrup, S. A., and Fitzhugh, E. L. (1995). Characteristics of brushpiles used by birds in Northern California. *Southwest. Nat.* 40, 86–93.

Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature* 242, 344–347.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., et al. (2008). Global change and the ecology of cities. *Science* 319, 756–760. doi: 10.1126/science.1150195

Hairston, N. G., Smith, F. E., and Slobodkin, L. B. (1960). Community structure, population control, and competition. *Am. Nat.* 94, 421–425.

Hammer, R. B., Stewart, S. I., Winkler, R. L., Radeloff, V. C., and Voss, P. R. (2004). Characterizing dynamic spatial and temporal residential density patterns from 1940–1990 across the North Central United States. *Landsc. Urban Plan.* 69, 183–199. doi: 10.1016/j.landurbplan.2003.08.011

Hsieh, T. C., Ma, K. H., and Chao, A. (2020). *iNEXT: iNterpolation and EXTrapolation for Species Diversity. R Package Version 2.0.20.* Available online at: http://chao.stat.nthu.edu.tw/wordpress/software-download/ (accessed May 1, 2020).

Hsieh, T. C., Ma, K. H., Chao, A., and McInerny, G. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451–1456. doi: 10.1111/2041-210X.12613

Hughes, J., and Macdonald, D. W. (2013). A review of the interactions between free-roaming domestic dogs and wildlife. *Biol. Conserv.* 157, 341–351. doi: 10.1016/j.biocon.2012.07.005

Ives, C. D., Lentini, P. E., Threlfall, C. G., Ikin, K., Shanahan, D. F., Garrard, G. E., et al. (2016). Cities are hotspots for threatened species. *Glob. Ecol. Biogeogr.* 25, 117–126. doi: 10.1111/geb.12404

Kays, R. W., and Parsons, A. (2014). Mammals in and around suburban yards, and the attraction of chicken coops. *Urban Ecosyst.* 17, 691–705. doi: 10.1007/s11252-014-0347-2

Kays, R. W., Parsons, A. W., Baker, M. C., Kalies, E. L., Forrester, T., Costello, R., et al. (2017). Does hunting or hiking affect wildlife communities in protected areas? *J. Appl. Ecol.* 54, 242–252. doi: 10.1111/1365-2664.12700

Lenth, B. E., Knight, R. L., and Brennan, M. E. (2008). The effects of dogs on wildlife communities. *Nat. Area. J.* 28, 218–227.

Lepczyk, C. A., Aronson, M. F. J., Evans, K. L., Goddard, M. A., Lerman, S. B., and MacIvor, J. S. (2017). Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. *Bioscience* 67, 799–807. doi: 10.1093/biosci/bix079

Liu, X., Huang, Y., Xu, X., Li, X., Li, X., Ciais, P., et al. (2020). High-spatiotemporal-resolution mapping of global urban change from 1985 to 2015. *Nat. Sustain.* 3, 564–570. doi: 10.1038/s41893-020-0521-x

Loss, S. R., Will, T., and Marra, P. P. (2013). The impact of free-ranging domestic cats on wildlife of the United States. *Nat. Commun.* 4:1396. doi: 10.1038/ncomms2380

Lowry, H., Lill, A., and Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549. doi: 10.1111/brv.12012

Magle, S., Theobald, D., and Crooks, K. (2009). A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. *Landsc. Ecol.* 24, 267–280. doi: 10.1007/s10980-008-9304-x

Mcdonald, R. I., Kareiva, P., and Forman, R. T. T. (2008). The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biol. Conserv.* 141, 1695–1703. doi: 10.1016/j.biocon.2008.04.025

McKee, C. J., Stewart, K. M., Sedinger, J. S., Bush, A. P., Darby, N. W., Hughson, D. L., et al. (2015). Spatial distributions and resource selection by mule deer in an arid environment: responses to provision of water. *J. Arid Environ.* 122, 76–84. doi: 10.1016/j.jaridenv.2015.06.008

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* 127, 247–260. doi: 10.1016/j.biocon.2005.09.005

McShea, W., Forrester, T., Costello, R., He, Z., and Kays, R. (2016). Volunteer-run cameras as distributed sensors for macrosystem mammal research. *Landsc. Ecol.* 31, 55–66. doi: 10.1007/s10980-015-0262-9

Murray, M. H., and St. Clair, C. C. (2017). Predictable features attract urban coyotes to residential yards. *J. Wildl. Manag.* 81, 593–600. doi: 10.1002/jwmg.21223

National Gardening Association (2014). *Garden to Table: A 5-Year Look at Food Gardening in America*. Burlington, VT: National Gardening Association.

Newsome, S. D., Garbe, H. M., Wilson, E. C., and Gehrt, S. D. (2015). Individual variation in anthropogenic resource use in an urban carnivore. *Oecologia* 178, 115–128. doi: 10.1007/s00442-014-3205-2

Ordeñana, M. A., Crooks, K. R., Boydston, E. E., Fisher, R. N., Lyren, L. M., Siudyla, S., et al. (2010). Effects of urbanization on carnivore species distribution and richness. *J. Mammal.* 91, 1322–1331. doi: 10.1644/09-MAMM-A-312.1

Parsons, A. W., Forrester, T., Baker-Whatton, M. C., McShea, W. J., Rota, C. T., Schuttler, S. G., et al. (2018). Mammal communities are larger and more diverse in moderately developed areas. *eLife* 7:e38012. doi: 10.7554/eLife.38012

Parsons, A. W., Rota, C. T., Forrester, T., Baker-Whatton, M. C., McShea, W. J., Schuttler, S. G., et al. (2019). Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. *J. Appl. Ecol.* 56, 1894–1904. doi: 10.1111/1365-2664.13385

Prange, S., Gehrt, S. D., and Wiggers, E. P. (2003). Demographic factors contributing to high raccoon densities in urban landscapes. *J. Wildl. Manag.* 67, 324–333.

Prevedello, J. A., Dickman, C. R., Vieira, M. V., and Vieira, E. M. (2013). Population responses of small mammals to food supply and predators: a global meta-analysis. *J. Anim. Ecol.* 82, 927–936. doi: 10.1111/1365-2656.12072

R Core Development Team (2019). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Reed, J. H., and Bonter, D. N. (2018). Supplementing non-target taxa: bird feeding alters the local distribution of mammals. *Ecol. Appl.* 28, 761–770. doi: 10.1002/eap.1683

Rodewald, A. D., Kearns, L. J., and Shustack, D. P. (2011). Anthropogenic resource subsidies decouple predator-prey relationships. *Ecol. Appl.* 21, 936–943. doi: 10.1890/10-0863.1

Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H., and Nilon, C. H. (2010). Invasion, competition, and biodiversity loss in Urban ecosystems. *Bioscience* 60, 199–208. doi: 10.1525/bio.2010.60.3.6

Soulsbury, C. D., and White, P. C. L. (2015). Human–wildlife interactions in urban areas: a review of conflicts, benefits and opportunities. *Wildl. Res.* 42, 541–553. doi: 10.1071/WR14229

Sperry, J. H., and Weatherhead, P. J. (2010). Ratsnakes and brush piles: intended and unintended consequences of improving habitat for wildlife? *Am. Midl. Nat.* 163, 311–317. doi: 10.1674/0003-0031-163.2.311

Su, Y., and Yajima, M. (2015). *R2jags: Using R to Run 'JAGS'. R package version 0.5-7.* Available online at: https://CRAN.R-project.org/package=R2jags (accessed February 1, 2020).

Sullivan, T. P. (1990). Responses of red squirrel (*Tamiasciurus hudsonicus*) populations to supplemental food. *J. Mammal.* 71, 579–590. doi: 10.2307/1381797

Trent, T. T., and Rongstad, O. J. (1974). Home range and survival of cottontail rabbits in Southwestern Wisconsin. *J. Wildl. Manag.* 38, 459–472. doi: 10.2307/3800877

U.S. Climate Data (2020). *Climate Raleigh-North Carolina*. Available online at: https://www.usclimatedata.com/climate/raleigh/north-carolina/united-states/usnc0558 (accessed March 24, 2020).

U.S. Department of the Interior, U.S. Fish and Wildlife Service, U.S. Department of Commerce, and U. S. Census Bureau. (2018). *2016 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation*. Washington, DC: U.S. Department of the Interior.

United Nations, Department of Economic and Social Affairs, Population Division (2017). *World Population Prospects: The 2017 Revision, Key Findings and Advance Tables. Working Paper no. ESA/P/WP/*248. New York, NY: ESA, 53.

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Behavior Change in Urban Mammals: A Systematic Review

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As cities expand to accommodate a growing human population, their impacts to natural ecosystems and the wildlife residing within them increase. Some animals that persist in urban environments demonstrate behaviors distinct from their non-urban counterparts. These potential behavioral changes are the subject of a growing body of research in the areas of wildlife ecology, biology, and conservation. In spite of increasing urban wildlife research, studies focused specifically on changing behavior in urban mammals is limited. We conducted a systematic literature review to synthesize current research on behavior changes in wild urban mammals. We included 83 papers published between 1987 and March 2020. Omnivores were the leading subject of study, closely followed by carnivores and the specific behaviors most widely studied were home range and vigilance. Among the reviewed studies, there were 166 observations of 44 distinct behaviors with 155 occurrences of behavior change relative to conspecifics in non-urban areas. The most commonly studied and observed type of behavior change was alert behavior. Results indicate urban environments drive adaptive responses in behavior including changes in home range and diet preference, shifts in activity budget and vigilance, decreased flight initiation distance, and increased nocturnal activity. Some urban mammal species even demonstrated the ability to modulate behaviors based on environmental cues. Our results highlight the need for long-term wildlife behavior studies across a variety of urban settings to promote successful urban wildlife management and conservation.

Keywords: acclimatory response, adaptive response, FID, home range, nocturnal activity, regulatory response, urban wildlife, behavioral syndrome

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INTRODUCTION

By 2050, 68% of the world's 9.7 billion people will be residing in urban areas (United Nations (UN) Department of Economic Social Affairs, 2019a; United Nations (UN) Department of Economic Social Affairs, 2019b). As cities expand to accommodate more people, their impacts to ecosystem processes and biota increase. Urban areas present unique and dynamic challenges for resident wildlife (Lowry et al., 2013; Miranda et al., 2013; Alberti, 2015; Birnie-Gauvin et al., 2016). In response to anthropogenic stressors, urban wildlife may exhibit behaviors differently than their non-urban counterparts (Ditchkoff et al., 2006; Chapman et al., 2012; DeCandia et al., 2019). As learning and behavioral adjustments are the primary ways animals cope with changing environments, the highly modified urban landscape provides a veritable proving ground for the ability of wildlife to adapt (Brown, 2012; Greggor et al., 2016). Decreasing natural habitat—alongside increasing anthropogenic resources—can lead to behavioral shifts in urban wildlife populations that present unique management and conservation challenges (Riley et al., 2010; Bateman and Fleming, 2012; Magle et al., 2019). Efforts to promote urban biodiversity while minimizing human-wildlife conflict will require a comprehensive understanding of what behavior changes are occurring in urban wildlife and how these species are potentially adapting over time.

Although behavior change can occur in wildlife without adaptation, it is helpful to consider behavioral responses, in terms of timescale and permanence, as either regulatory, acclimatory, or developmental (Lopez-Sepulcre and Kokko, 2012; McDonnell and Hahs, 2015). Where behavior changes fall among these three categories of adaptative response can offer insight into the mechanisms of change and whether behaviors may revert to population norms or progress toward permanent adaptation (Dingemanse et al., 2010; McDonnell and Hahs, 2015). Regulatory responses such as changes in alert behavior like harm avoidance or decreased flight initiation distance (FID) often develop within seconds to hours, whereas acclimation (e.g., adjustments in social structures and territoriality) may develop gradually over days and weeks (Bateman and Fleming, 2012; McDonnell and Hahs, 2015). Physiological changes and behavioral syndromes such as neophilia and boldness may indicate more permanent developmental response potentially leading to evolutionary change (Dingemanse et al., 2010; Lopez-Sepulcre and Kokko, 2012; McDonnell and Hahs, 2015). These adaptive responses may complement species survivability in some cases while being detrimental in others (Lopez-Sepulcre and Kokko, 2012; Lowry et al., 2013; Robertson, 2018; Ellington and Gehrt, 2019). As humans continue to alter the habitat and resources available to urban wildlife, knowing how these animals are adapting their behavior is key to understanding how certain species will persist in urban environments (Ryan and Partan, 2014; Soulsbury and White, 2015).

Despite urbanization's significant impact on wildlife, urban wildlife research remains a young and poorly understood field (Birnie-Gauvin et al., 2016; Magle et al., 2019). In their review of urban wildlife research, Magle et al. (2012) found that urban wildlife studies comprised 2% of total publication volume. Although animal behavior is a common research topic and behavioral changes between urban and non-urban conspecifics are somewhat widely studied, mammals have been underrepresented (Magle et al., 2012; Miranda et al., 2013; McDonnell and Hahs, 2015; Schell, 2018). This is somewhat surprising as changes in mammalian behavior can often be precursors to conflict with humans and understanding how mammals use urban areas is an important component of wildlife management (Gehrt and McGraw, 2007; Karelus et al., 2017). Although selective urban pressures can have contrasting effects among mammalian species, it appears that behavioral flexibility among mammals allows them to better adapt to the urban environment (Santini et al., 2019). Generally, mammals are easily disturbed by human activity which drive changes in their behavior that can impact diet, reproduction, stress levels, dial activity, and disease prevalence (Ditchkoff et al., 2006; Birnie-Gauvin et al., 2016). These changes can lead to adaptations that may have important eco-evolutionary consequences. Despite the importance of understanding behavior changes in urban mammals, there has been no comprehensive review of the current primary literature specific to urban mammal behavior.

Following PRISMA guidelines, we conducted a systematic literature review of research pertaining to urban mammal behavior conducted over the past five decades. The aim of this review was to synthesize all research generating significant findings of behavior change in urban mammal populations (*population*) that were conducted in an urban setting, including those using conspecific and predator decoys, human-interaction, camera trap, trap and release, and/or remote tracking protocols (*interventions*) to assess behavior change comparative to a non-urban population as defined by each individual study (*comparator*). Further, we sought to coalesce all research identifying specific behavior change (*outcomes*) in urban mammal populations, whether these changes were assessed via direct observation or inferred from remotely sensed/spatial data (*study designs*). Specifically, we were interested in the extent of urban mammal behavior change research and what, taken together, this research reveals in terms of adaption to the urban environment. In answering this research question, we unveil the predominate types of behavioral adjustments observed in urban mammals, which taxa were most studied, the journals that publish these studies, geographically where these studies were conducted, and how these trends might inform future research. Our findings underscore the importance of long-term behavioral studies to fully understand how short-term behavior changes become more permanent adaptations and to better inform urban wildlife management decisions ranging from conservation to human-wildlife co-existence.

METHODS

To quantify the body of research specific to behavioral change in urban mammals, we conducted a systematic literature review following Pullin et al. (2018) using Web of Science and Google Scholar. We searched Web of Science for papers in the primary literature using the following search terms and Boolean operators: "urban*,", "city," "town" OR "metro;" "animal," "wild*," OR "mammal;" "beh*;" and "chang*," "mod*," "adapt*," "alter*" OR "evol*." For Google Scholar, we used multiple combinations of primary search terms (urban, animal, behavior, change, mammal, and wildlife) in various sub-sections (e.g., "in the title," "anywhere," "in subject"). Specific search parameters can be found in **Supplementary Table 1**. We also reviewed citations within each retained paper for additional relevant studies.

We first compared titles to eliminate redundancy from our two searches. We included or excluded papers using pre-defined inclusion/exclusion criteria (**Table 1**) based on the title and/or abstract. For each study retained, we recorded how data was collected, study region, and the season each study took place. We also recorded species information, behavior studied, whether there was a change in behavior, the direction of effect where appropriate, and the type of adaptation demonstrated by the behavior change. We used the non-evolutionary adaptive responses identified by Ricklefs (1990) to group observed behavior changes into one of three adaptive response categories:

TABLE 1 | Criteria used to determine inclusion/exclusion of articles for literature review.

INCLUSION	
Behavior study	Article must be a behavior study; note, spatial studies may be appropriate if there is a stated behavior associated with observed change (e.g., home range)
Urban population	Article must study behavior of a species/population in an urban setting
Comparative behavior	Articles must study behavior of urban population with comparative reference (either results from same study on a different population or from literature) to indicate behavior adaptation (e.g., rural vs. urban)
Relevant species	Article must include behavior study on at least one species in the class Mammalia
Publication	Must be from a peer-reviewed publication; graduate theses may be included if quality of study is appropriate
Language	Article must be either published in English or reliably translated
Gray literature	Must provide relevant information specific to urban mammal behavior change
EXCLUSION	
Irrelevant species	Articles on urban animal behavior adaptation in solely non-mammalian and non-wild species (e.g., domestic or feral animals)
Presence/ absence/ abundance studies	Articles solely on species abundance, presence or absence of species in urban areas
Non-urban	Articles that do not include behavior demonstrated specifically in the urban environment (i.e., studies conducted along an urban-rural gradient may be included but will be excluded if at least one study area is not expressly urban)
Literature review	Reviews of literature or publications that do not include novel study results
Laboratory study	Articles on urban mammalian behavior observed in a laboratory setting
Author duplication	Multiple articles written by the same author(s) with the same observed behavior change if it is clear that observations were from the same study/data
Unavailability	Articles not available through university resources, general internet access, etc.

regulatory, acclimatory, or developmental (McDonnell and Hahs, 2015).

RESULTS

Our *Web of Science* search resulted in 640 records, and *Google Scholar* yielded 136 for a total of 776 records. After removing duplicates, we were left with 744 unique records. After applying inclusion/exclusion criteria, we were left with 65 papers from our database searches. We then reviewed the citations within each retained paper and found an additional 18 papers that met our inclusion criteria for a final total of 83 studies (**Supplementary Figure 1**). These 83 studies spanned from 1987 to 2020 and represent 8 general publication categories (**Figure 1**). The studies were predominately published in journals specific to zoology and mammalogy.

The region with the greatest number of studies was North America (n = 43, 52%), followed by Europe (n = 17, 20.5%), Australia (n = 9, 11%), Asia (n = 7, 8.5%), Africa (n = 5, 6%), and South America (n = 2, 2%). With respect to diet guilds, 44% of the studies were on omnivores (n = 37), 40% were on carnivores (n = 33), and 16% were on herbivores (n = 13). Every region with the exception of South America had studies from each of these three guilds (**Figure 2**).

Although most of the 83 studies focused on one species, 3 included observations on 2 or more species. Overall, 45 mammalian species were studied across 10 orders: Carnivora (n = 37 studies, 43%), Rodentia (n = 23 studies, 26%), Primate (n = 7 studies, 8%), Artiodactyla (n = 5 studies, 6%), Chiroptera (n = 4 studies, 5%), Diprotodontia (n = 4 studies, 5%), Lagomorpha (n = 3 studies, 3%), Didelphimorphia (n = 2 studies, 2%), Eulipotyphla (n = 1 study, 1%), and Peramelemorphia (n = 1 study, 1%). The four most studied species were coyote (*Canis latrans*; n = 12; 27%); eastern gray squirrels (*Sciurus carolinensis*; n = 5, 11%); Eurasian red squirrels (*Sciurus vulgaris*, n = 5, 11%); and black bears (*Ursus americanusi*, n = 5, 11%).

Behaviors Studied

Some studies assessed multiple behaviors, which resulted in 166 observations of 44 different behaviors (**Supplementary Table 2**). Studied behaviors fell into 8 general types: alert behavior (n = 45; 27.1%), spatial (n = 40, 24.1%), diet preference/foraging/resource use (n = 27, 16.3%), activity budget (n = 22, 13.3%), diel activity (n = 14, 8.4%), behavioral syndrome (n = 9, 5.4%), mating/reproduction (n = 7, 4.2%), and social (n = 2, 1.2%) (**Figure 3**). With respect to taxa, all orders included at least one spatial behavior study, with the exception of primates (**Supplementary Figures 2, 3**). Of the two most studied orders, researchers primarily looked at alert behavior in Rodentia (n = 25/45) and spatial behavior in Carnivora (n = 22/40).

Behavior Change

Of the 166 studied behaviors, 93% (n = 155) were different from those observed in conspecifics outside the urban setting. In the remaining observations (n = 11; 7%), researchers found no change in behavior when comparing urban and non-urban mammal populations. Behavior changes were observed across all 10 orders (**Table 2**) and in almost every species studied (n = 41; 91%) with the exception of Merriam's kangaroo rat (*Dipodomys merriami*) and 3 bats (*Lasionycteris noctivagans*, *Myotis spp.*, and *Eptesicus fuscus*). Among the studies that observed changes in behavior, the direction of change was not always consistent, even among species (**Supplementary Table 2**, Column: "Change"). In addition, some researchers observed multi-directional shifts in behavior in response to varying environmental stimuli (n = 7, 4%).

Adaptive Response

Acclimation was the most common type of adaptive response (n = 105; 68% of total behavior changes) observed among all taxa in the reviewed studies (**Supplementary Table 3**). Six

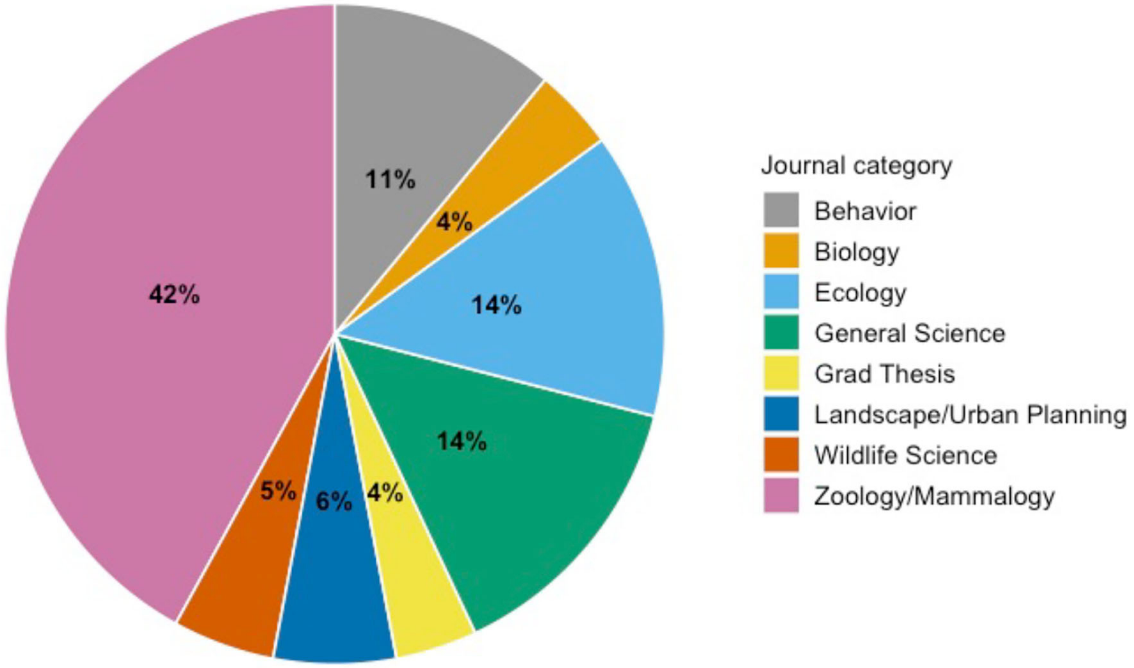

FIGURE 1 | Publication categories of journals that published urban mammal behavior change studies between 1987 and 2020 with percentages of papers in each category.

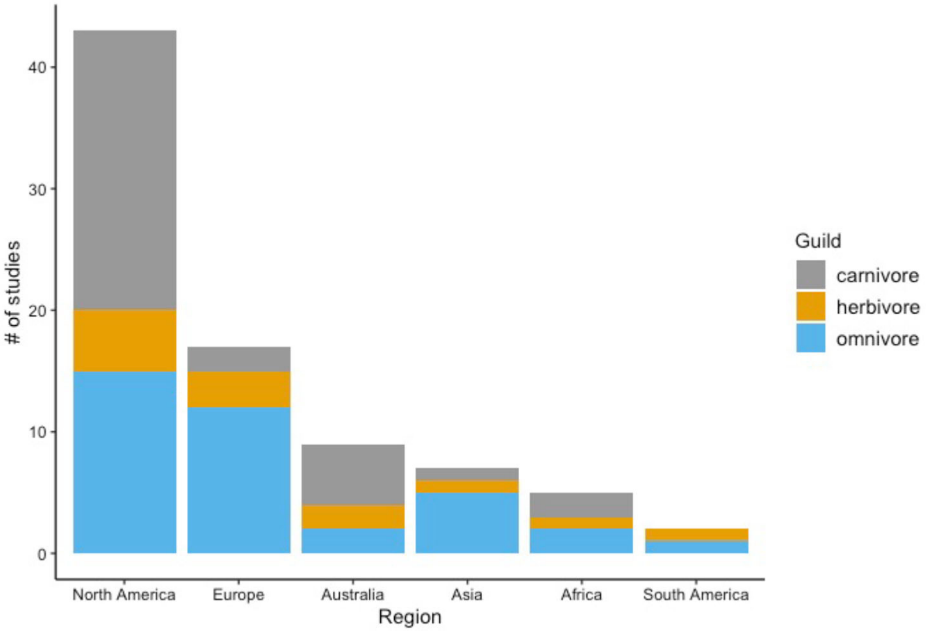

FIGURE 2 | The number of studies that assessed behavioral changes of urban mammals across 6 world continents between 1987 and 2020. Results are categorized by diet guild.

of the 8 types of behavior change (activity, diel, diet/resource use, mating/reproduction, social, and spatial) reflect acclimatory response to the urban environment (**Figure 4**). Of these, decreased home range (*n* = 19; 18% of total acclimatory responses) was the most frequently observed, followed by increased nocturnality (*n* = 9; 9%), diet preference changes (*n* = 9; 9%), and shift in resource selection (*n* = 9; 9%). All observed changes in alert behavior were categorized as regulatory

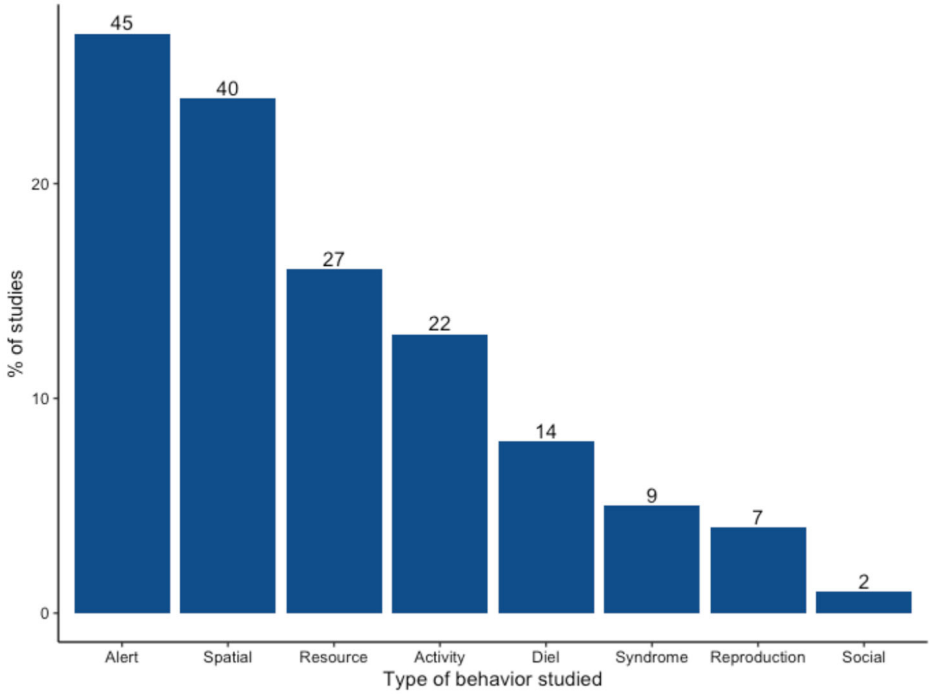

FIGURE 3 | Types of behavior changes studied in urban mammals between 1987 and 2020. Values above bars indicate the total number of observations studied within each behavior type.

responses ($n = 43$; 28% of total behavior changes). The most common regulatory responses were changes in vigilance/caution behavior ($n = 11$, 4 decreasing, 5 increasing, 2 shifting with no direction noted; 26% of total regulatory behavior changes) and decreased FID ($n = 9$; 21%). Observations of syndrome behavior in urban mammals indicate developmental response to the urban environment ($n = 7$; 5% of total behavior changes). The two most prevalent changes in syndrome behavior were increased boldness ($n = 3$; 43% of total developmental behaviors) and increased exploratory behavior ($n = 3$; 43%). Together, omnivores, carnivores, and herbivores demonstrate more acclimatory response to the urban environment than regulatory and developmental responses, combined (**Figure 5**).

DISCUSSION

Our results clearly demonstrate that mammals are responding to the urban environment by changing their behavior. Much less clear is what these changes mean in terms of urban mammalian diversity, survivability, management, and conservation. Although the reported behavior changes reflect various types of adaptive response, the studies do not consistently discuss underlying mechanisms or their potential evolutionary implications. The vast majority of studies documented some degree of behavior change, but findings differed in terms of scale and direction—often depending on region, species, or resource availability. These results suggest there are varying mechanisms behind adaptive behavioral responses in urban mammals and that the nuances of these behavior shifts require further exploration.

Research Extent

In-line with previous reviews, our results indicate that urban wildlife research is an emerging field and just recently gaining attention (Miranda et al., 2013; Magle et al., 2019). We found only 83 studies that explicitly studied mammalian behavior change in urban settings, and 50% of those studies were conducted in the last 5 years. Similarly, a previous review on overall urban wildlife behavior found 9 studies published between 1987 and 2012 that reported changes in alert and syndrome behavior in urban mammals (Miranda et al., 2013). That number increased to 50 in our review. Although this rapid jump is promising, the taxa remains significantly underrepresented, especially when compared to research on avian species in the urban environment (Miranda et al., 2013; Sol et al., 2013; McDonnell and Hahs, 2015). Given the negative impact that urbanization has on mammalian biodiversity (McCleery, 2010), and that the presence of mammals in urban areas often results in conflict with humans (Santini et al., 2019), it is important that future urban wildlife research reflects extant mammal populations in the respective region of study.

Taxonomic Focus

Although mammals are an underrepresented taxonomic group in urban wildlife research, our review indicates a greater variety of mammalian species are being studied ($n = 45$) as compared to previous reviews (Ditchkoff et al., 2006; Miranda et al., 2013; Sol et al., 2013; McDonnell and Hahs, 2015). Although the number

TABLE 2 | Behavior changes found in urban mammals grouped by order and guild.

Order	Guild	Behavior change
Artiodactyla (11)	carnivore (2) herbivore (3) omnivore (6)	Anti-predator, avoidance, FID (flight initiation distance), vocalization, home range, nocturnality, resource selection, spatial patterns, travel distance
Carnivora (62)	carnivore (53) omnivore (9)	AD (alert distance), anti-predator, avoidance, FID (flight initiation distance), escape activity, vigilance/caution, activity budget, den selection, denning time, diet preference, dispersal, fecundity, foraging/hunting, home range, movement speed, nocturnality, resource selection, spatial patterns, territoriality, time encamped, time/distance traveling, time foraging, boldness, exploratory
Chiroptera (2)	carnivore (2)	Home range, time foraging
Didelphimorphia (3)	omnivore (3)	Home range, travel distance
Diprotodontia (5)	carnivore (3) herbivore (2)	Vigilance/caution, diet preference, home range
Eulipotyphla (3)	omnivore (3)	Avoidance, spatial patterns, diel activity
Lagomorpha (7)	herbivore (7)	Anti-predator, vigilance/caution, activity budget, latrine use, spatial patterns, time resting
Peramelemorphia (1)	omnivore (1)	Home range
Primate (18)	herbivore (8) omnivore (10)	Anti-predator, vigilance/caution, activity budget, conspecific tolerance, diet preference, foraging/hunting, grooming, play, problem-solving, time feeding, time resting, time traveling, exploratory
Rodentia (43)	herbivore (4) omnivore (39)	AD (alert distance), alarm behavior, alert response, anti-predator, concealment distance, FID (flight initiation distance), vigilance/caution, VED (vertical escape distance), activity budget, den selection, denning time, diet preference, dispersal, diurnality, foraging/hunting, GUD (giving-up density), home range, latency, resource selection, spatial patterns, time foraging, aggression

Values in parentheses indicate the number of behavior changes observed.

of mammalian species has expanded, squirrel (n = 12) and coyote ($n = 12$) remain the dominate focal species, comprising almost a third of all studies. Likewise, herbivores were not well-represented ($n = 31$; 19%). Notably, deer (family *Cervidae*) and raccoon (*Procyon lotor*) made rare appearances in reviewed studies. Only one species of deer was represented (*Odocoileus virginianus*) in two studies (Harveson et al., 2007; Gallo et al., 2019) and we found only a single study (Prange et al., 2004) assessing urban racoon behavior change. As deer and raccoons are commonly associated with conflict in urban environment (Curtis and Hadidian, 2010; Hadidian et al., 2010; Westerfield et al., 2019), we were surprised at the apparent lack of interest in their behavior which does not align with on-the-ground management needs (Prange et al., 2003; Urbanek et al., 2011). These findings highlight the persistent gap between animal behavior research and management action, while underscoring the need for urban mammal behavior research that is responsive to management and conservation concern (Caro, 1999; Curtis and Hadidian, 2010; McDonnell and Hahs, 2015; Greggor et al., 2016). Further, increasing taxa representation in this research will establish a foundational understanding of species-specific behavior change which can illuminate the degree and rate of urban-driven behavioral adaptation.

Changing Behavior and Adaptative Response

The most common type of adaptive behavioral response observed was acclimatory. This is not surprising as the acclimatory category encompasses behaviors relating to movement, activity, and resource use, all of which were well-represented in the reviewed studies. Urban mammals are widely adapting to the urban environment by acclimating their movement and resource use patterns. In every study assessing home range ($n = 25$), a change was observed when compared to non-urban populations. The majority (76%) of studies on home range found that these decreased for urban mammals. However, the direction of effect was not consistent, even among the same species. As an example, the home range of urban lesser Asiatic yellow bats varied by sex: the home range of female bats increased in urban areas, while urban males decreased their home range (Atiqah et al., 2015). Conversely, 50% of studies on canids found that coyotes and fox (*Vulpes vulpes*) decreased their home range while 40% had an increased home range; the other 10% did not demonstrate a change in home range size *per se*, but a shift in terms of drifting territory or habitat type within the respective range (Doncaster and Macdonald, 1991; Grinder and Krausman, 2001; Gehrt et al., 2009; Grubbs and Krausman, 2009; Rosatte and Allan, 2009; Gese et al., 2012; Poessel et al., 2016; Ellington and Gehrt, 2019). One explanation for inconsistent changes in urban mammal home ranges could be the highly variable nature of urban environments including inconsistent resource availability (Fitzgibbon et al., 2011; Wright et al., 2012; Bateman and Fleming, 2014; Van Helden et al., 2018). Urban mammals may selectively seek out natural prey, even among abundant anthropogenic resources which can drive increased home ranges in some mammals (Newsome et al., 2015). As population densities of mammals tend to be relatively high in urban areas, understanding behaviors that impact movement patterns and resource use can be key to successful management and conservation strategies (Curtis and Hadidian, 2010; Riley et al., 2010).

Although behavioral acclimations reveal much about mammalian adaptation to urban pressures, they do not reflect the full array of immediate behavioral response to urban stimuli, nor longer-term developmental change (McDonnell and Hahs, 2015). As examples, alert response and behavioral syndromes respectively provide insight into regulatory and developmental adaptations, both with important evolutionary implications (Sih et al., 2004; Dingemanse et al., 2010; Réale et al., 2010). Altered anti-predator behavior in the urban environment can significantly alter activity budgets and energy

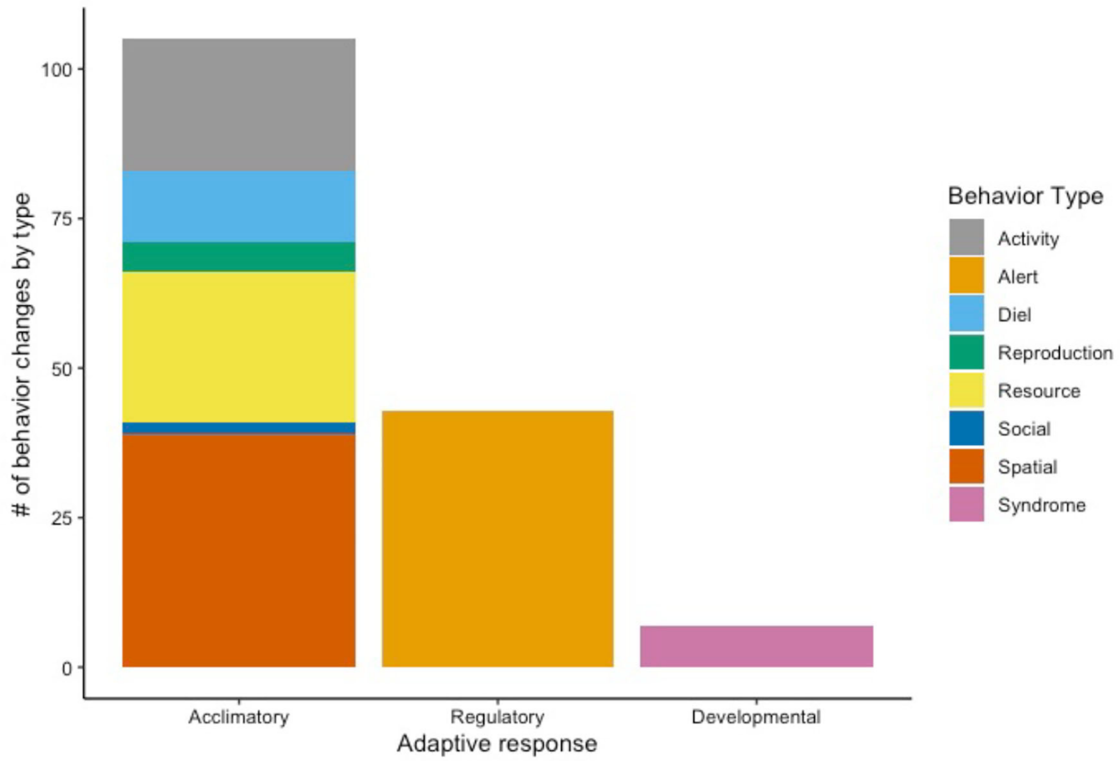

FIGURE 4 | The 8 types of behavior changes observed in urban mammals from 1987 to 2020 categorized by adaptive response.

stores (Réale et al., 2010). Consistent behavior modifications across different urban stimuli (i.e., behavioral syndromes such as increased boldness) can likewise impact mortality risk (Luttbeg and Sih, 2010). Each of the three types of adaptation (acclimatory, regulatory, developmental) offer useful clues as to how the urban environment affects mammal populations and how it may drive evolutionary change (Miranda et al., 2013; McDonnell and Hahs, 2015; Greggor et al., 2019). As such, increased research on behaviors that reflect a broader array of regulatory and developmental adaptions will result in a more comprehensive understanding of the mechanisms behind urban mammal behavior change. Taking a collective look across the full temporal range of behavioral adaptation may help predict how urban mammal populations will fare in the face of continued urbanization. Beneficial behavior modifications by founder individuals can lead to increased fitness, whereas other adaptations may decrease survivability, both of which can result in higher-order effects on population dynamics among urban species (Lopez-Sepulcre and Kokko, 2012; Pelletier and Garant, 2012; Alberti, 2015; Birnie-Gauvin et al., 2016; Schell, 2018). Further, urban pressures and other drivers (e.g., anthropogenically provided food) that impact eco-evolutionary feedbacks appear to affect the distribution of behavioral traits (Alberti, 2015; Schell, 2018). Regulatory, acclimatory, and developmental adaptations all have the potential to alter processes that undermine healthy ecosystems and biodiversity, both of which are already fundamentally challenged in the urban environment (Palkovacs and Dalton, 2012; Alberti, 2015; McDonnell and Hahs, 2015). Continued research on how urban mammal behaviors are adapting across all timescales can yield important insights for conservationists, wildlife managers, city planners, and urban residents alike.

Modulating Behavior

Because urban environments present such a dynamic mix of threats, it stands to reason that some changes in mammal behavior are multi-directional and perhaps, fluctuating. A particularly interesting finding among a small number of studies ($n = 7/166$) is that some mammals demonstrate the ability to modulate adapted responses based on environmental cues. For example, two studies found variation in vigilance levels of individual woodchucks (*Marmota monax*) based on the intensity of urbanization, possibly reflecting the variable nature of human pressures in highly urbanized areas (Watson, 2010; Lehrer et al., 2012). Likewise, fox squirrels (*Sciurus niger*) in Texas, USA demonstrated the ability to modulate anti-predator behavior to cope with constant stimuli created by humans in the urban environment (McCleery, 2009). Partan et al. (2010), found that eastern gray squirrels in western Massachusetts, USA modulated their alert behavior by increasing their reliance on visual signals vs. audio signals in noisier environments. A study in New York, United States, found that 90% of urban gray

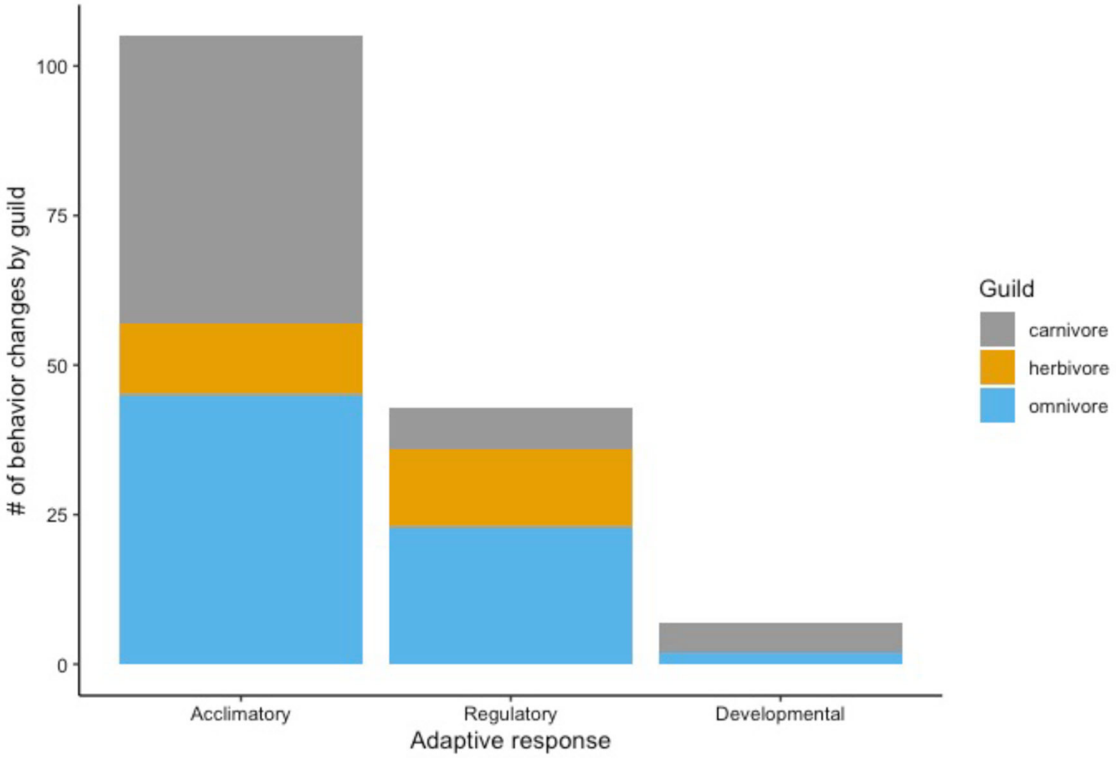

FIGURE 5 | The number of behavior changes by diet guild in urban mammals from 1987 to 2020 categorized by adaptive response.

squirrels increased their FID when approached by humans that veered off the sidewalk and looked at them, while squirrels from the same population did not increase FID if approaching humans remained on the sidewalk (Bateman and Fleming, 2014). Likewise, urban Eurasian red squirrels demonstrated the ability to assess risk levels of various approaching objects (e.g., humans and conspecific decoys) and modulated their FID accordingly (Uchida et al., 2019, 2020). Finally, a study on Australian fur seals (*Arctocephalus pusillus doriferus*) found that seals modulated their alert response based on vessel type and whether or not vessels conformed with mandated approach distance thresholds—indicating that the seals learned the legal distance ships were able to approach (Speakman et al., 2020).

It is not readily apparent from these studies whether the modulations demonstrated are a function of inter-individual differences (behavioral plasticity) or consistent behavioral adaptations in response to repeated urban stimuli but they are all linked to risk assessment which has significant survival, and thus, evolutionary implications (Réale et al., 2010; Lopez-Sepulcre and Kokko, 2012; Bateman and Fleming, 2014). Although these represent a small sample size of reviewed studies, these apparent behavior modulations could begin to explain the behavior change pattern variation among certain urban mammal species. Seemingly, the majority of studies were designed to record discrete behavioral responses to specific stimuli and may have simply missed, or not considered, modulating behaviors. More research should focus on how urban mammals modulate their behaviors in response to variable urban pressures to better inform the drivers of urban-driven evolutionary behavior change. Understanding the mechanisms behind modulating adaptive behaviors, whether behavioral plasticity or contemporary evolution, can provide important insight into urban ecosystem ecology (Palkovacs and Dalton, 2012; Miranda et al., 2013; McDonnell and Hahs, 2015).

Limitations and Recommendation for Future Research

In our review, we did not establish a specific definition of "urban." Instead, we relied on the authors' designation of the research setting as such. This inherently introduces limitations in capturing information about how varying levels of urbanization impact behavior change in mammals. Definitions of "urban" in the reviewed studies, and elsewhere, are broad and may not consistently consider factors such as land use, structures, human population density, and impervious surfaces (McIntyre et al., 2008; Bateman and Fleming, 2012; Alldredge et al., 2019; Ellington and Gehrt, 2019). Thus, we were unable to reliably relate specific features of urbanization to observed changes in behavior.

As raccoon and deer conflict is relatively common in urban settings (Hadidian et al., 2010; Westerfield et al., 2019), it was odd to us that so little of the research focused on these species. Like McDonnell and Hahs (2015), we recommend future urban mammal research focus on delivering specific solutions to conservation and management challenges. Knowing how urban mammals are changing their behavior can improve mitigation strategies and conservation interventions (Caro, 1999; Greggor et al., 2016). Urban mammal researchers should continue to look at a host of behaviors that reflect various types of adaptive response (i.e., regulatory, acclimatory, and developmental) as they may be interrelated or lead to potential adaptative evolution over time (McDonnell and Hahs, 2015). Future research should highlight potential causes for observed adaptive responses to gain a better understanding of the mechanisms underlying urban mammal behavior change (Palkovacs and Dalton, 2012; Greggor et al., 2016). Conducting long-term, parallel studies on specific behaviors across a host of cities could likewise illuminate regional trends and help identify variable mechanisms driving behavior changes in the urban setting (Magle et al., 2019; Santini et al., 2019).

CONCLUSION

Animal behavior is changing in urban environments and the long-term effects of these changes are unknown. This literature review demonstrates that urban mammals are exhibiting widespread acclimatory behavioral response to urban pressures. Our findings suggest a need to better understand the mechanisms behind urban mammal behavior change and the eco-evolutionary impacts that may result. Although a relatively nascent area of study, urban mammal research requires a shift to align priorities in a way that contributes to the growing body of knowledge on changing behavior while supporting real-time management and conservation efforts. To fully understand changing urban mammal behavior, long-term studies across multiple cities will better inform local wildlife management solutions, establish baselines of species-specific behavior change, and promote the mutually beneficial co-existence of all urban residents.

DATA AVAILABILITY STATEMENT

The original contributions generated for the study are included in the article/**Supplementary Materials**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

KR and TG conceptualized the study, collected data, and wrote the manuscript.

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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.2020.576665/full#supplementary-material

REFERENCES

Alberti, M. (2015). Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol. Evol.* 30, 114–126. doi: 10.1016/j.tree.2014.11.007

Alldredge, M. W., Buderman, F. E., and Blecha, K. A. (2019). Human-Cougar interactions in the wildland-urban interface of Colorado's front range. *Ecol. Evol.* 9, 10415–10431. doi: 10.1002/ece3.5559

Atiqah, N., Akbar, Z., Syafrinna, Ubaidah, N., and Foo, N. Y. (2015). "Comparison of the ranging behavior of *Scotophilus kuhlii* (Lesser Asiatic Yellow Bat) in agricultural and urban landscape," in *AIP Conference Proceedings*, Vol. 1678 (Bandar Baru Bangi: AIP Publishing LLC), 020026.

Bateman, P. W., and Fleming, P. A. (2012). Big city life: carnivores in urban environments. *J. Zool.* 287, 1–23. doi: 10.1111/j.1469-7998.2011.00887.x

Bateman, P. W., and Fleming, P. A. (2014). Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *J. Zool.* 294, 93–98. doi: 10.1111/jzo.12156

Birnie-Gauvin, K., Peiman, K. S., Gallagher, A. J., De Bruijn, R., and Cooke, S. J. (2016). Sublethal consequences of urban life for wild vertebrates. *Environ. Rev.* 24, 416–425. doi: 10.1139/er-2016-0029

Brown, C. (2012). "Experience and learning in changing environments," in *Behavioural Responses to a Changing World: Mechanisms and Consequences*, eds U. Candolin and B. B.M. Wong (Oxford: Oxford University Press), 46–62.

Caro, T. (1999). The behaviour–conservation interface. *Trends Ecol. Evol.* 14, 366–369. doi: 10.1016/S0169-5347(99)01663-8

Chapman, T., Rymer, T., and Pillay, N. (2012). Behavioural correlates of urbanisation in the cape ground squirrel Xerus inauris. *Naturwissenschaften* 99, 893–902. doi: 10.1007/s00114-012-0971-8

Curtis, P. D., and Hadidian, J. (2010). "Responding to human-carnivore conflicts in urban areas," in *Urban Carnivores: Ecology, Conflict, and Conservation*, eds S. D. Gehrt, S. P. D. Riley, and B. L. Cypher (Baltimore, MA: The Johns Hopkins University Press), 223–232.

DeCandia, A. L., Brzeski, K. E., Heppenheimer, E., Caro, C. V., Camenisch, G., Wandeler, P., et al. (2019). Urban colonization through multiple genetic lenses: the city-fox phenomenon revisited. *Ecol. Evol.* 9, 2046–2060. doi: 10.1002/ece3.4898

Dingemanse, N. J., Kazem, A. J., Réale, D., and Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* 25, 81–89. doi: 10.1016/j.tree.2009.07.013

Ditchkoff, S. S., Saalfeld, S. T., and Gibson, C. J. (2006). Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosyst.* 9, 5–12. doi: 10.1007/s11252-006-3262-3

Doncaster, C. P., and Macdonald, D. W. (1991). Drifting territoriality in the red fox *Vulpes vulpes*. *J. Anim. Ecol.* 423–439. doi: 10.2307/5288

Ellington, E. H., and Gehrt, S. D. (2019). Behavioral responses by an apex predator to urbanization. *Behav. Ecol.* 30, 821–829. doi: 10.1093/beheco/arz019

Fitzgibbon, S. I., Wilson, R. S., and Goldizen, A. W. (2011). The behavioural ecology and population dynamics of a cryptic ground-dwelling mammal in an urban Australian landscape. *Austral. Ecol.* 36, 722–732. doi: 10.1111/j.1442-9993.2010.02209.x

Gallo, T., Fidino, M., Lehrer, E. W., and Magle, S. (2019). Urbanization alters predator-avoidance behaviours. *J. Anim. Ecol.* 88, 793–803. doi: 10.1111/1365-2656.12967

Gehrt, S. D., Anchor, C., and White, L. A. (2009). Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *J. Mammal.* 90, 1045–1057. doi: 10.1644/08-MAMM-A-277.1

Gehrt, S. D., and McGraw, M. (2007). "Ecology of coyotes in urban landscapes," in *Wildlife Damage Management Conferences Proceedings*. Available online at: https://digitalcommons.unl.edu/icwdm_wdmconfproc/63

Gese, E. M., Morey, P. S., and Gehrt, S. D. (2012). Influence of the urban matrix on space use of coyotes in the Chicago metropolitan area. *J. Ethol.* 30, 413–425. doi: 10.1007/s10164-012-0339-8

Greggor, A. L., Berger-Tal, O., Blumstein, D. T., Angeloni, L., Bessa-Gomes, C., Blackwell, B. F., et al. (2016). Research priorities from animal behaviour for maximising conservation progress. *Trends Ecol. Evol.* 31, 953–964. doi: 10.1016/j.tree.2016.09.001

Greggor, A. L., Trimmer, P. C., Barrett, B. J., and Sih, A. (2019). Challenges of learning to escape evolutionary traps. *Front. Ecol. Evol.* 7:408. doi: 10.3389/fevo.2019.00408

Grinder, M. I., and Krausman, P. R. (2001). Home range, habitat use, and nocturnal activity of coyotes in an Urban environment. *J. Wildl. Manage.* 65, 887–898. doi: 10.2307/3803038

Grubbs, S. E., and Krausman, P. R. (2009). Use of urban landscape by coyotes. *Southwest. Nat.* 54, 1–12. doi: 10.1894/MLK-05.1

Hadidian, J., Prange, S., Rosatte, R., Riley, S. P. D., and Gehrt, S. D. (2010). "Raccoons (Procyon lotor)," in *Urban Carnivores: Ecology, Conflict, and Conservation*, eds S. D. Gehrt, S. P. D. Riley, and B. L. Cypher (Baltimore, MA: The Johns Hopkins University Press), 35–47.

Harveson, P. M., Lopez, R. R., Collier, B. A., and Silvy, N. J. (2007). Impacts of urbanization on Florida key deer behavior and population dynamics. *Biol. Conserv*. 134, 321–331. doi: 10.1016/j.biocon.2006.07.022

Karelus, D. L., McCown, J. W., Scheick, B. K., van de Kerk, M., Bolker, B. M., and Oli, M. K. (2017). Effects of environmental factors and landscape features on movement patterns of Florida black bears. *J. Mammal.* 98, 1463–1478. doi: 10.1093/jmammal/gyx066

Lehrer, E. W., Schooley, R. L., and Whittington, J. K. (2012). Survival and antipredator behavior of woodchucks (*Marmota monax*) along an urban-agricultural gradient. *Can. J. Zool.* 90, 12–21. doi: 10.1139/z11-107

Lopez-Sepulcre, A., and Kokko, H. (2012). "Understanding behavioural responses and their consequences," in *Behavioural Responses to a Changing World: Mechanisms and Consequences*, eds U. Candolin and B. B.M. Wong (Oxford: Oxford University Press), 280.

Lowry, H., Lill, A., and Wong, B. B. (2013). Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549. doi: 10.1111/brv.12012

Luttbeg, B., and Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 3977–3990. doi: 10.1098/rstb.2010.0207

Magle, S. B., Fidino, M., Lehrer, E. W., Gallo, T., Mulligan, M. P., Ríos, M. J., et al. (2019). Advancing urban wildlife research through a multi-city collaboration. *Front. Ecol. Environ*. 17, 232–239. doi: 10.1002/fee.2030

Magle, S. B., Hunt, V. M., Vernon, M., and Crooks, K. R. (2012). Urban wildlife research: past, present, and future. *Biol. Conserv*. 155, 23–32. doi: 10.1016/j.biocon.2012.06.018

McCleery, R. (2010). Urban mammals. *Urban Ecosyst. Ecol.* 55, 87–102. doi: 10.2134/agronmonogr55.c5

McCleery, R. A. (2009). Changes in fox squirrel anti-predator behaviors across the urban–rural gradient. *Landsc. Ecol.* 24:483–493. doi: 10.1007/s10980-009-9323-2

McDonnell, M. J., and Hahs, A. K. (2015). Adaptation and adaptedness of organisms to urban environments. *Annu. Rev. Ecol. Evol. Syst.* 46, 261–280. doi: 10.1146/annurev-ecolsys-112414-054258

McIntyre, N. E., Knowles-Yánez, K., and Hope, D. (2008). "Urban ecology as an interdisciplinary field: differences in the use of "urban" between the social and natural sciences," in *Urban Ecology* (Boston, MA: Springer), 49–65.

Miranda, A. C., Schielzeth, H., Sonntag, T., and Partecke, J. (2013). Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Glob. Chang. Biol.* 19, 2634–2644. doi: 10.1111/gcb.12258

Newsome, S. D., Garbe, H. M., Wilson, E. C., and Gehrt, S. D. (2015). Individual variation in anthropogenic resource use in an urban carnivore. *Oecologia* 178, 115–128. doi: 10.1007/s00442-014-3205-2

Palkovacs, E. P., and Dalton, C. M. (2012). "Ecosystem consequences of behavioural plasticity and contemporary evolution," in *Behavioural Responses to a Changing World Mechanisms and Consequences* (Oxford: Oxford University Press), 175–189.

Partan, S. R., Fulmer, A. G., Gounard, M. A. M., and Redmond, J. E. (2010). Multimodal alarm behavior in urban and rural gray squirrels studied by means of observation and a mechanical robot. *Curr. Zool.* 56, 313–326. doi: 10.1093/czoolo/56.3.313

Pelletier, F., and Garant, D. (2012). "Population consequences of individual variation in behaviour," in *Behavioural Responses to a Changing World* (Oxford: Oxford University Press), *159*—174.

Poessel, S. A., Breck, S. W., and Gese, E. M. (2016). Spatial ecology of coyotes in the denver metropolitan area: influence of the urban matrix. *J. Mammal*. 97, 1414–1427. doi: 10.1093/jmammal/gyw090

Prange, S., Gehrt, S. D., and Wiggers, E. P. (2003). Demographic factors contributing to high raccoon densities in urban landscapes. *J. Wildlife Manag.* 67, 324–333. doi: 10.2307/3802774

Prange, S., Gehrt, S. D., and Wiggers, E. P. (2004). Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *J. Mammal*. 85, 483–490. doi: 10.1644/BOS-121

Pullin, A., Frampton, G., Livoreil, B., and Petrokofsky, G., (eds.). (2018). *Guidelines and Standards for Evidence Synthesis in Environmental Management*. Collaboration for Environmental Evidence. Available online at: http://www.environmentalevidence.org/information-for-authors (accessed October 1, 2019).

Réale, D., Dingemanse, N. J., Kazem, A. J., and Wright, J. (2010). *Evolutionary and ecological approaches to the study of* personality. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 365, 3937–3946. doi: 10.1098/rstb.2010.0222

Ricklefs, R.E. (1990). *Ecology*, *3rd Edn.* New York, NY: Freeman.

Riley, S. P. D., Gehrt, S. D., and Cypher, B. L. (2010). "Urban carnivores: final perspectives and future directions," in *Urban Carnivores: Ecology, Conflict, and Conservation*, eds S. D. Gehrt, S. P. D. Riley, and B. L. Cypher (Baltimore, MA: The Johns Hopkins University Press), *223*—232.

Robertson, K. E. (2018). *Boldness Behavior and Chronic Stress in Free-Ranging, Urban Coyotes (Canis latrans).* (Ph.D. thesis), The Ohio State University. Available online at: http://rave.ohiolink.edu/etdc/view?acc_num=osu1543529587211372

Rosatte, R., and Allan, M. (2009). The ecology of red foxes, vulpes vulpes. Metropolitan Toronto, Ontario: disease management implications. *Canad. Field Nat.* 123, 215–220. doi: 10.22621/cfn.v123i3.967

Ryan, A. M., and Partan, S. R. (2014). "Urban wildlife behavior," in *Urban Wildlife Conservation* (Boston, MA: Springer), 149–173.

Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A., and Ancillotto, L. (2019). One strategy does not fit all: determinants of urban adaptation in mammals. *Ecol. Lett.* 22, 365–376. doi: 10.1111/ele.13199

Schell, C. J. (2018). Urban evolutionary ecology and the potential benefits of implementing genomics. *J. Heredity* 109, 138–151. doi: 10.1093/jhered/esy001

Sih, A., Bell, A., and Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* 19, 372–378. doi: 10.1016/j.tree.2004.04.009

Sol, D., Lapiedra, O., and González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Anim. Behav*. 85, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Soulsbury, C. D., and White, P. C. (2015). Human–wildlife interactions in urban areas: a review of conflicts, benefits and opportunities. *Wildlife Res*. 42, 541–553. doi: 10.1071/WR14229

Speakman, C. N., Johnstone, C. P., and Robb, K. (2020). Increased alertness behavior in Australian fur seals (*Arctocephalus pusillus doriferus*) at a high vessel traffic haul-out site. *Mar. Mamm. Sci*. 36, 486–499. doi: 10.1111/mms.12654

Uchida, K., Shimamoto, T., Yanagawa, H., and Koizumi, I. (2020). Comparison of multiple behavioral traits between urban and rural squirrels. *Urban Ecosyst.* 23, 745–754. doi: 10.1007/s11252-020-00950-2

Uchida, K., Suzuki, K. K., Shimamoto, T., Yanagawa, H., and Koizumi, I. (2019). Decreased vigilance or habituation to humans? mechanisms on increased boldness in urban animals. *Behav. Ecol.* 30, 1583–1590. doi: 10.1093/beheco/arz117

United Nations (UN) Department of Economic and Social Affairs, Population Division. (2019a). *World Urbanization Prospects: The 2018 Revision (ST/ESA/SER.A/420).* Available online at: https://population.un.org/wup/Publications/Files/WUP2018-Report.pdf. (accessed 28 May 2020).

United Nations (UN) Department of Economic and Social Affairs, Population Division. (2019b). *World Population Prospects 2019: Highlights (ST/ESA/SER.A/423).* Available online at: https://www.un.org/development/desa/publications/world-population-prospects-2019-highlights.html. (accessed 28 May 2020).

Urbanek, R. E., Allen, K. R., and Nielsen, C. K. (2011). Urban and suburban deer management by state wildlife-conservation agencies. *Wildlife Soc. Bull.* 35, 310–315. doi: 10.1002/wsb.37

Van Helden, B. E., Speldewinde, P. C., Close, P. G., and Comer, S. J. (2018). Use of urban bushland remnants by the western ringtail possum (*Pseudocheirus occidentalis*): short-term home-range size and habitat use in Albany, Western Australia. *Aust. Mammal.* 40:173. doi: 10.1071/AM17026

Watson, E. L. (2010). Effects of urbanization on survival rates, anti-predator behavior, and movements of woodchucks (*Marmota monax*). Available online at: http://hdl.handle.net/2142/14642

Westerfield, G. D., Shannon, J. M., Duvuvuei, O. V., Decker, T. A., Snow, N. P., Shank, E. D., et al. (2019). Methods for managing human–deer conflicts in urban, suburban, and exurban areas. *Hum. Wildlife Inter. Monogr.* 3, 1–99. Available online at: https://digitalcommons.usu.edu/hwi_monographs/3/. (Accessed on 16 2020).

Wright, J. D., Burt, M. S., and Jackson, V. L. (2012). Influences of an Urban environment on home range and body mass of virginia opossums (*Didelphis virginiana*). *Northeastern Nat.* 19, 77–86. doi: 10.1656/045.019.0106

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Big City Living: A Global Meta-Analysis Reveals Positive Impact of Urbanization on Body Size in Lizards

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Urban environments pose different selective pressures than natural ones, leading to changes in animal behavior, physiology, and morphology. Understanding how animals respond to urbanization could inform the management of urban habitats. Non-avian reptiles have important roles in ecosystems worldwide, yet their responses to urbanization have not been as comprehensively studied as those of mammals and birds. However, unlike mammals and birds, most reptiles cannot easily move away from disturbances, making the selective pressure to adapt to urban environments especially strong. In recent years, there has been a surge in research on the responses of lizards to urbanization, yet no formal synthesis has determined what makes an urban lizard, in other words, which phenotypic traits are most likely to change with urbanization and in which direction? Here, we present a qualitative synthesis of the literature and a quantitative phylogenetic meta-analysis comparing phenotypic traits between urban and non-urban lizard populations. The most robust finding from our analysis is that urban lizards are larger than their non-urban counterparts. This result remained consistent between sexes and taxonomic groups. Hence, lizards that pass through the urban filter have access to better resources, more time for foraging, and/or there is selection on attaining a larger body size. Other results included an increase in the diameters of perches used and longer limb and digit lengths, although this may be a result of increased body size. Urban lizards were not bolder, more active or exploratory, and did not differ in immune responses than non-urban populations. Overall, studies are biased to a few geographic regions and taxa. More than 70% of all data came from three species of anoles in the family *Dactyloidae*, making it difficult to generalize patterns to other clades. Thus, more studies are needed across multiple taxa and habitats to produce meaningful predictions that could help inform conservation and management of urban ecological communities.

Keywords: ectotherm, evidence synthesis, human induced environmental change, meta-regression, urban ecology, urban evolution

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INTRODUCTION

We live in the Anthropocene, an epoch in which humans are now the major driver of global environmental change (Lewis and Maslin, 2015; Biermann et al., 2016). Urbanization is one of the most extreme forms of human-induced environmental change and has progressed rapidly in recent years. In 2007, for the first time in human history, more people were living in cities than in rural areas, and it is expected that more than 65% of the human population will be urban by the year 2050 (United Nations, 2019). Cities drastically change the abiotic and biotic features of the environment, creating strong, and sometimes novel, selection pressures on native flora and fauna. Impervious surface cover (e.g., concrete) is greatly increased in cities which affects the water cycle, albedo, and temperature, often leading to the "urban heat island" effect (Grimm et al., 2008; Hulley, 2012). Urban habitats tend to be more open, with fewer trees (LaMontagne et al., 2015) and with human-constructed substrates that are more broad and smooth than natural substrates (Winchell et al., 2018). Habitat fragmentation due to urbanization could lead to depressed diversity and abundance of native species, including a reduction in natural predator populations, altering the ecological relationships within communities (McKinney, 2008; Dobbs et al., 2017). These anthropogenic impacts are apparent in cities around the world, demonstrating the potential to use these systems as replicated natural experiments to study the ecological and evolutionary implications of urbanization on wildlife (Johnson and Munshi-South, 2017).

Urban selection pressures, like those listed above, have led to shifts in behavioral, morphological, and physiological responses in animals. Urban animals tend to be more bold in response to reduced predation pressure and a habituation to human presence (Møller, 2009; Samia et al., 2015; Symonds et al., 2016). Urban birds and frogs shift their singing/calling frequencies to reduce overlap with anthropogenic sounds (Roca et al., 2016), while urban mammals have become more nocturnal to reduce overlap of activity times with humans (Gaynor et al., 2018). In response to the urban heat island effect, many species, from ants to anoles, have evolved higher physiological tolerance of high temperatures (Angilletta et al., 2007; Brans et al., 2017; Campbell-Staton et al., 2020). Shifts in morphological traits are also commonly reported; for instance urban insects are generally smaller in body size (Merckx et al., 2018; Eggenberger et al., 2019), urban bats and birds tend to have higher wing aspect ratios (Croci et al., 2008; Voigt and Kingston, 2015; Santini et al., 2019), and urban birds show changes in beak depth and length (Giraudeau et al., 2014; Miller et al., 2018) compared to their non-urban counterparts. These are just a few examples of differences in animal phenotypes that have been and continue to be documented in urban environments.

Shifts in animal phenotypes associated with urbanization occur at higher rates than those due to other forms of anthropogenic disturbances (Alberti et al., 2017). Many species and populations have demonstrated remarkable abilities to survive and reproduce within habitats that have been drastically altered by humans, yet not all have the capabilities to do so (i.e., many species are filtered out; Hamer and McDonnell, 2008; Schochet et al., 2016; Silva et al., 2016; Santini et al., 2019). While it is possible for rapid evolution to occur on timescales that are relevant to urbanization, shifts in phenotypic traits are more likely the result of phenotypic plasticity (Kinnison and Hendry, 2001; Miranda et al., 2013; Nelson et al., 2015), and/or spatial sorting of individuals across urban-rural landscapes whereby individuals with certain traits are more likely to disperse into urban habitats while individuals lacking these traits remain in non-urban habitats (Berthouly-Salazar et al., 2012; Piano et al., 2017). Additionally, some phenotypes, like body size, might not change due to selection, but rather are a consequence of shifting resource types or availabilities. In most cases, observed changes in phenotypes cannot yet be specifically attributed to changes in gene frequency or expression (McDonnell and Hahs, 2015), although some studies find support for rapid genetic responses to urban environments [reviewed in Johnson and Munshi-South (2017)]. Understanding how organisms respond to urbanization will allow us to predict which species, populations, or individuals are most vulnerable, providing valuable information for curbing the loss of wildlife during the Anthropocene (Dirzo et al., 2014).

Reviews, syntheses, and multi-species assessments on the phenotypic responses of animals to urbanization have largely centered around birds (Chamberlain et al., 2009; Evans et al., 2011; Seress and Liker, 2015; Kettel et al., 2018; Martin and Bonier, 2018) and mammals (Benítez-López et al., 2010; Ordeñana et al., 2010; Saito and Koike, 2013; Voigt and Kingston, 2015; Łopucki and Kitowski, 2017). Yet, an increase in research on non-avian reptiles (henceforth "reptiles") has the potential to expand our knowledge on wildlife responses to urbanization, which could better inform the management and conservation of ecological communities in urban areas. Similar to mammals and birds, reptiles are mostly terrestrial vertebrates that serve important roles in the ecosystems where they occur (de Miranda, 2017). However, the functional significance of reptiles often differs substantially from that of mammals and birds due to their different thermoregulatory strategies (Nowak et al., 2008; Jessop et al., 2020). In turn, their responses to urbanization are likely to differ. Unlike mammals and birds, reptiles tend to have relatively low dispersal abilities, and so they may be more likely to experience selection from rapid human-induced habitat changes. As ectotherms, reptiles might be more sensitive to the urban thermal environment than mammals or birds. They also utilize habitats differently (e.g., climbing on human-made structures) and are likely susceptible to different suites of predators and parasites.

Research on the effects of urbanization on reptiles has increased considerably in the last 5 to 10 years. A handful of recent reviews have attempted to synthesize this nascent literature (French et al., 2018; Lapiedra, 2018; Putman et al., 2019b). While many unique reptilian responses to urbanization have been documented, directionality seems to be largely variable (likely due to the heterogeneity of urban environments and differences among species) with very few overall trends. Behaviorally, urban species seem to display more neophilic and risk-taking behavior, however, where domestic predators (especially cats) are present, flight initiation distance tends to increase (French et al., 2018; Putman et al., 2019b). Some species have shown higher rates of morphological asymmetry and increased limb length and body size, often accompanying changes in habitat use (e.g., perch selection and tendency to jump between perches vs. moving about on the same perch; French et al., 2018; Lapiedra, 2018). All authors agree that significant gaps in the literature persist regarding the mechanisms that drive specific responses within urban systems, the relationships between responses and fitness, and the relationships between responses at different levels of ecological organization.

The majority of research within the field of urban herpetology has focused on lizards (all clades within the order *Squamata* excluding *Serpentes* and *Amphisbaenia*), likely because lizards have historically been used as models in research on behavior, ecology, and evolution. Lizards are also ideal for comparative studies as they are widely distributed, physiologically and morphologically diverse, tolerant of experimental procedures and handling, and the life histories of many species are well-understood (Camargo et al., 2010). While many individual studies on various urban lizard populations have been investigated, no generalizations can be drawn as to what makes an urban lizard because no quantitative synthesis at the global scale has been conducted. A recent meta-analysis found that human-induced habitat modifications have had negative impacts on reptile populations worldwide (Doherty et al., 2020), yet information regarding traits of successful species will be useful in predicting other species' responses and for the holistic management of urban ecological communities. In order to fill this information gap, here we qualitatively review the state of the literature within this field of urban herpetological research and take a comparative phylogenetic approach to analyze published data on the effects of urbanization on the physiological, morphological, or behavioral traits in lizards worldwide.

METHODS

Literature Search

Our goal was to determine the impacts of urbanization on behavioral, physiological, and/or morphological traits in lizards. We performed a literature search on 23 May 2019, using the University of California, Los Angeles institutional subscriptions. Our search contained all years of publication. Within Web of Science, we searched the Core Collection, BIOSIS Previews, and Zoological Record. We used the following search terms: (lizard* OR gecko* OR agama* OR chameleon* OR iguan* OR anol* OR tegu* OR whiptail* OR skink* OR dragon*) AND (urban* OR suburb* OR anthropogenic OR city OR cities OR village* OR town* OR municipalit* OR neighborhood* OR industrializ* OR "human impact" OR "human built" OR "human modified" OR "human altered") AND (behavior OR morphology OR physiology). We also searched ProQuest for unpublished data in dissertations and theses, and verified that the data presented in these were not already published in the peer-reviewed literature. In ProQuest, we searched on title and abstract only (no full text) using the same search terms as above. Finally, when conference proceedings were found, we searched to see if the research had been published in the peer-reviewed literature. Three reviews were found and we reviewed their references to verify that the searches above did not miss any additional relevant publications.

Study Selection

The study selection process followed PRISMA guidelines (Moher et al., 2009, **Figure 1**). The initial search yielded 1,700 unique records, including two from published reviews. We removed duplicates, which narrowed down the total to 1,336 records. Next, we reviewed papers on their titles and abstracts. We set criteria based on PICOs (population, intervention, comparator, outcome) of traditional systematic reviews to decide whether studies met eligibility for being included in our syntheses. Articles were deemed relevant if the study population was a lizard species, if the study compared at least one urban and one non-urban population of the same species (intervention of urbanization and comparator of urban "treatment" vs. non-urban "control"), and if the study quantified a behavioral, morphological, or physiological trait (outcome). We were only interested in papers that focused solely on urbanization, and not other forms of anthropogenic disturbances such as logging or agriculture. We recognize the lack of globally universal criteria used to define urban areas from rural areas and so we relied on authors' descriptions of their study sites along with the objectives of their study (i.e., if the goal was to compare an urban population with a non-urban one) to determine relevance for inclusion. In five cases we had to determine ourselves whether a study fit our comparator inclusion criterion. For this, we used a liberal definition of

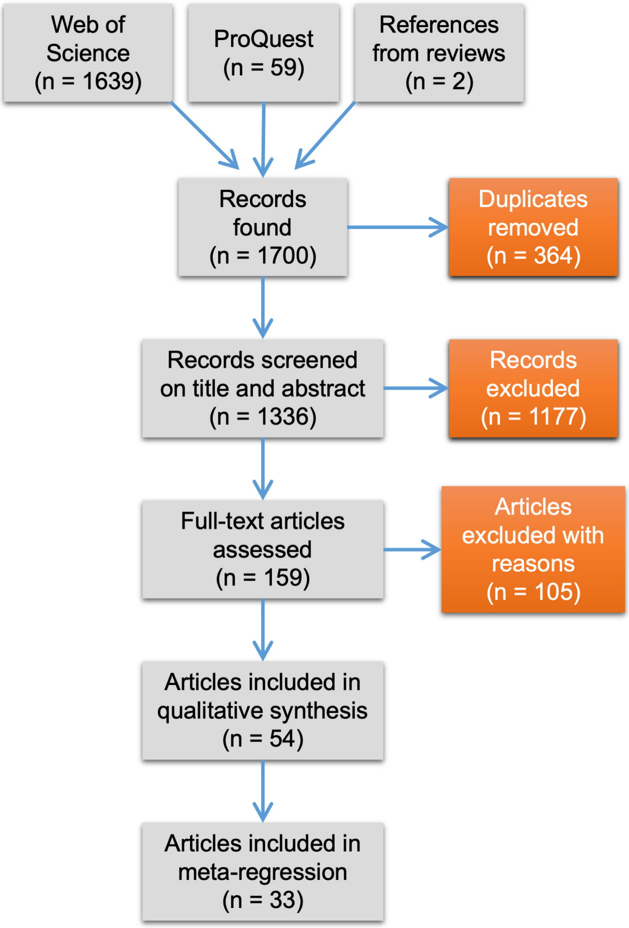

FIGURE 1 | PRISMA flow diagram showing number of articles retrieved from the literature search and retained or excluded during the study selection process.

urbanization that is related to the functional characteristics of urban areas, such as the existence of buildings, paved roads, electrical and sewage systems, and other urban infrastructure [see United Nations (2019)]. We considered a lizard population urban if it occurred in an area with these urban functional characteristics regardless of the human population density or density of buildings. Non-urban lizard populations occurred in areas that lacked such characteristics. We acknowledge that this added heterogeneity to our dataset, and we tried to account for this in the analyses below.

The removal of studies lacking an urban to non-urban comparator narrowed down our total to 159 papers (**Supplementary Table 1** shows all relevant studies and reasons for exclusion). Full text screening was then conducted using the same inclusion criteria as above. We emailed authors when we could not access their articles or when data were not presented in a way useful for a meta-analysis (i.e., no means reported). Seven out of 14 authors that were emailed replied and graciously supplied the missing information. Finally, we also excluded studies not published in the English language as this is the only language we are proficient in. In all, 54 articles were available for data extraction (**Supplementary Tables 1, 2**). We used these 54 articles to perform a qualitative synthesis of current foci and practices in urban lizard research. In this synthesis, we included information on focal species and traits studied, and information on the study attributes listed below.

Data Extraction

For all studies, we extracted the raw means and variances (e.g., standard deviation) of the measured phenotypic trait(s). We used the WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/) to extract data presented in figures. We also scored the following variables: (1) taxonomic information such as family, genus, and species, (2) sex of population studied (as female, male, or both), (3) name of urban locality (e.g., city or metropolitan area) to account for differences associated with year and/or intensity of urbanization, and (4) study attributes including location, duration, and number of replicate sites. Some papers reported results on more than one species, quantified multiple phenotypic traits, quantified traits under different treatments, and/or reported results from multiple localities (e.g., different cities), and each of these were considered as different entries in the database (i.e., there can be multiple entries per article). When papers reported separate traits by sex (e.g., body sizes of males and of females separately), these were also considered different entries. We only included results from adult or sub-adult lizards as only a handful of studies focused on hatchling or juvenile traits (i.e., these studies were not included in the quantitative analysis).

We extracted data on behavioral, morphological, or physiological traits. Studies focused on various traits within each of these broad phenotypic categories, listed in **Figure 2** and **Supplementary Table 2**. Traits were further refined based on specific assays used to estimate them; for instance, limb length can be measured multiple ways including total hind limb length, femur length, tibia/fibula length, forelimb length, etc. We made an effort to create biologically meaningful categories and erred on the side of splitting traits based on assays used to measure them instead of lumping means from multiple assays together. As an example, we split boldness into three categories (escape responses, willingness to be exposed, and latency to respond to stimuli) as we felt each of these represent bold behaviors under different circumstances or motivational states.

Statistical Analyses

We performed a phylogenetic meta-analysis, specifically a meta-regression, to statistically evaluate the effects of urbanization on lizard traits. In order to be included in this analysis, a phenotypic trait category had to contain a minimum of 10 estimates (i.e., 10 effect sizes) as this sample size allows for correct quantification of between-study variance (Nakagawa et al., 2017). These included 18 traits: 5 measures of behavior, 10 measures of morphology (mainly different assays of limb and digit lengths), and 3 measures of physiology/health (**Supplementary Table 3** shows the full database). To examine the mean effects of urbanization on these traits, we calculated the standardized mean difference (SMD) as Hedges' *g* (Hedges, 1981). Although the log response ratio (lnRR) is another statistic of effect size commonly used in ecology and evolutionary biology (Borenstein et al., 2009), we could not compute this because our database contained instances of means with opposing signs. When applicable, we adjusted the signs of effect size estimates so that positive values indicate a positive shift in the trait with urbanization (e.g., when boldness is measured as latency to emerge from refuge lower values indicate higher boldness).

We followed the methods of Mallen-Cooper et al. (2019) for the statistical analyses. We used the "metaphor" package in R (Viechtbauer, 2010; R version 3.6.1) to perform a meta-regression to evaluate heterogeneity among effect sizes. We fitted a multilevel model with the *rma.mv* function. We included study (article) and id (different effect sizes) as random factors to account for between-study effects and within-study effects, respectively. We added urban locality (e.g., city or metropolitan area) as a random effect to account for variation attributable to time since and/or intensity of urbanization. We also added species and phylogeny as random effects. To control for potential non-independence from phylogenetic relatedness, we used a correlation matrix derived from an ultrametric tree of squamate reptiles from Pyron et al. (2013) assuming a Brownian-motion model of evolution (**Supplementary Figure 1**). Inclusion of these five random effects helps identify additional sources of variance besides sampling error, and hence they are considered variance components in the model.

We included phenotypic trait as a moderator variable (fixed effect), and we calculated true intercepts and standard errors for each trait so that results reflect group means rather than contrasts to a reference group. We did this by running the model without an intercept so that all dummy variables are included as predictors. We used confidence intervals to evaluate statistical significance; a result was deemed significant if the interval did not include zero. Publication biases were evaluated using a funnel plot, Egger's test for asymmetry, and the trim and fill method (Nakagawa and Santos, 2012). A post-model fitting check was also performed to assess whether the full model was

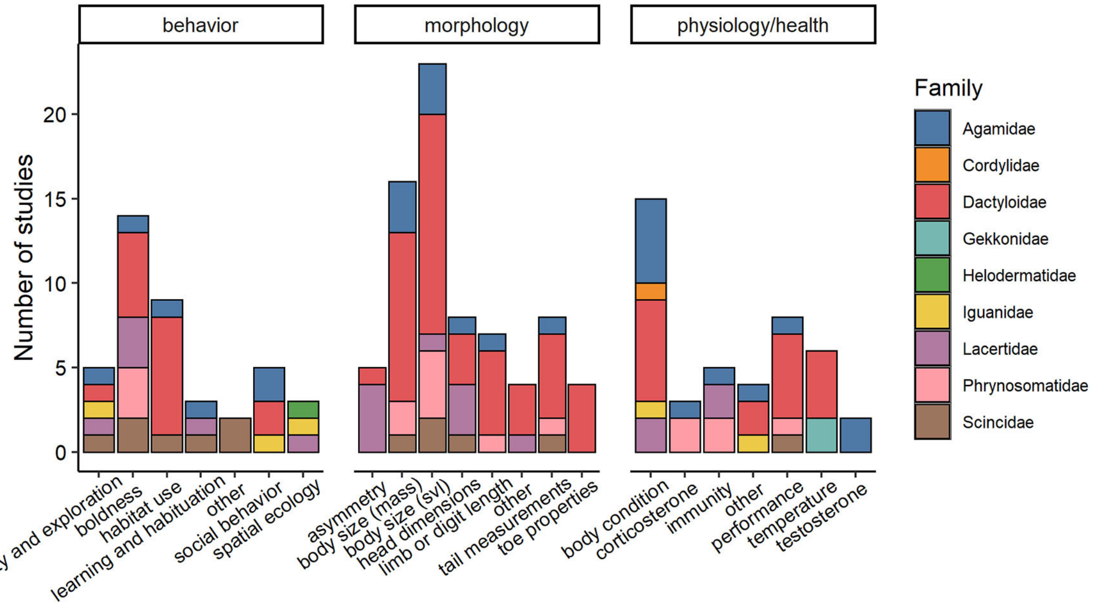

FIGURE 2 | Number of studies on urban lizards categorized by type of phenotypic trait and by family ($N = 54$ articles; each article may have more than one study). Only a few behavioral, morphological, and/or physiological traits have been quantified and within only nine lizard families. Snout-vent-length, a measure of lizard body length, is abbreviated to svl.

overparameterized. We created profile plots of the restricted log-likelihood as a function of each variance component (random effects; Konstantopoulos, 2011).

In addition to the above model, we ran models with reduced data sets to evaluate the robustness of the results. First, we recognized that multiple studies had measured the same traits from the same individuals multiple ways or under multiple treatments contributing to pseudoreplication in the database. As examples, Winchell et al. (2016) measured lower forelimb length as both the length of the ulna and length of the radius (from the same individual), and Lapiedra et al. (2017) measured boldness in the same individuals as latency to appear out of a refuge, latency to emerge from the refuge, and latency to climb on a perch. In all these instances, the estimates were highly correlated. Although we included study as a random effect to partially account for this, this still does not entirely remove this source of non-independence. Thus, when studies reported multiple estimates of the same trait from the same set of individuals, we only included one of these estimates and removed the others. We selected to include the estimate that was measured most-closely to the majority of the other traits in the same phenotypic category. For instance, we selected to include data on ulna length from Winchell et al. (2016) and remove data on radius length because most of the other studies within the lower forelimb category reported estimates of ulna length. This process lead to the removal of 74 effect sizes (12%) from the database, 16% from activity and exploration, 10% from boldness (exposure), 28% from boldness (latency), 7% from digit length (forelimb), 33% from digit length (hind limb), 11% from immunity, 26% from limb length (radius/ulna), 23% from limb length (tibia/fibula), and 38% from performance (**Supplementary Table 4** shows the reduced database).

Furthermore, we performed subgroup analyses to determine the influence of particular groupings on the results. We were specifically interested in the effects of sex (i.e., were responses more or less pronounced in males?). Unfortunately, the only trait for which we could evaluate sex differences in responses was for body size (measured as snout-vent-length, svl). All other traits did not have adequate sample sizes of effect sizes, especially for female lizards (65% of all effect sizes came from males and 21% of effect sizes were from the sexes pooled). Thus, we ran a meta-regression model on body size (svl) effect sizes and set sex as the moderator variable (removing estimates from the sexes pooled so that we could assess males and females separately). We included the same random effects as above.

We also assessed the influence of *Anolis* lizards (family Dactyloidae), which contributed to ~75% of all effect sizes in the database, in driving the results. We removed all effect sizes associated with *Anolis* lizards and ran this reduced meta-regression model with trait as a moderator and the same random effects as above. However, this model only included the traits of body size (svl) and immunity as the removal of *Anolis* effect sizes made most traits unsuitable for analysis due to too small of sample sizes. Thus, in all, we could only look at the influence of sex and taxonomic bias using the body size (svl) trait data.

RESULTS

Qualitative Synthesis

The number of studies published on lizards in urban environments has substantially grown in just the past 5

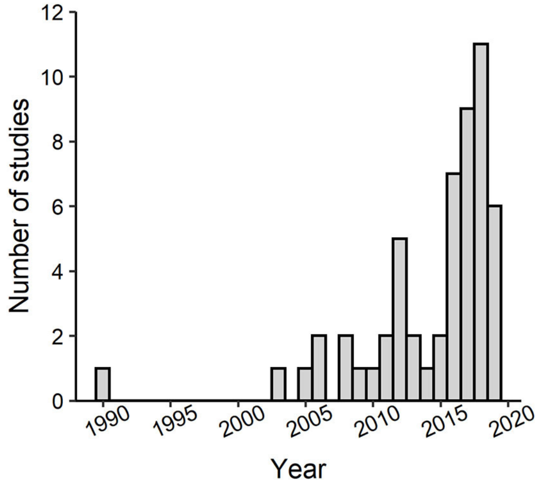

FIGURE 3 | Histogram showing the number of studies produced per year for the past 30 years (each bar represents a single year) that have investigated effects of urbanization on lizard phenotypic traits. The bar associated with 2019 does not include all studies from that year because our literature search was conducted in May of 2019.

years (**Figure 3**). Yet, studies have been narrowly focused on only 22 different species in 9 families (**Figure 2**) even though lizards represent ∼9% of all vertebrate life on Earth (Uetz, 2020). The vast majority of studies have been conducted on anoles in the family *Dactyloidae*. Specifically, *Anolis cristatellus* was the most studied species with roughly half of the studies on this species occurring in Miami, Florida, where this species is invasive. The remaining studies on this species occurred in Puerto Rico, where it is native. Studies have been geographically biased (**Figure 4**). Studies conducted in Puerto Rico and mainland United States contributed the most effects toward our analysis (111 and 105 effect sizes, respectively), with studies in Australia contributing the third most effects with only 20 effect sizes. Thus, we lack data from most continents even though lizards occur on every one except Antarctica. Effects from male lizards outnumbered effects from females and mixed sex samples combined (168, 44, and 62 effect sizes, respectively). Body size (as svl) was the most commonly reported phenotype with 40 effects from 21 of the studies, and morphology, in general, was the most commonly reported phenotype followed by behavior (192 and 62 effect sizes, respectively). Number of replicate sites used in each study ranged from 1–7, with an average of 2.5 urban sites, and non-urban replicates were slightly fewer with an average of 2.4 sites. Most studies were conducted in a single year (61%), but the overall range was 1–9 years.

Quantitative Meta-Analysis

The effects of urbanization have led to significant increases in lizard body size (svl and mass) and limb and digit lengths, and a significant increase in the diameters of perches used (**Figure 5A**, **Table 1**). There was a marginal increase in running performance (sprint speed) with urbanization, but this was not significant in the reduced model when pseudoreplicated effect sizes were removed (**Figure 5B**, **Table 1**). Urbanization had large effects (SMD > 0.8) on body mass and the diameters of perches used, and medium effects (SMD > 0.5) on measures of limb length (except for humerus length), on measures of digit length, and on body length (svl). Urbanization did not affect two estimates of boldness (willingness to be exposed and latency to respond to stimuli), perch height, activity and exploration, body condition, or immune responses of lizards.

We found high heterogeneity ($I^2 = 95.2\%$) in our meta-regression model. The effects of urbanization on lizard traits were largely unrelated to phylogenetic relatedness of the lizard species ($I^2_{[\text{phylogeny}]} < 0.01\%$), and were similar within species ($I^2_{[\text{species}]} = 5.7\%$), but urban locality displayed high variance ($I^2_{[\text{locality}]} = 59.9\%$), along with high variance at the effect size level ($I^2_{[\text{residual}]} = 18.7\%$). There was moderate between-study variance ($I^2_{[\text{study}]} = 11.0\%$). When assessing publication bias, we found that although the Egger's test revealed asymmetry in our data set ($z = 3.290$, $P = 0.001$), the trim and fill function indicated that no studies were missing from the left-hand side of the funnel plot ($P = 0.500$, **Supplementary Figure 2**). All five profile plots for the variance components peaked at the respective parameter (REML) estimates and the log-likelihoods quickly decreased as the values of the components moved away from the estimates, indicating that the variance components were identifiable and our model was not overparameterized (**Supplementary Figure 3**).

When effect sizes from *Anolis* lizards were removed from the database, results on body size (svl) and immunity still held, with non-anoline lizards showing an increase in body size with urbanization (estimate ± SE: 0.594 ± 0.241, 95% CI: 0.122–1.066) and no shift in immune responses (estimate ± SE: 0.355 ± 0.269, 95% CI: −0.172–0.881). We found no effect of sex on body size: urbanization leads to larger body sizes in both female (estimate ± SE: 0.579 ± 0.252, 95% CI: 0.085–1.074) and male lizards (estimate ± SE: 0.703 ± 0.206, 95% CI: 0.300–1.107).

DISCUSSION

Our knowledge on the effects of urbanization in lizards is still in its infancy. We show that studies are biased toward certain taxa, certain geographical locations, and we lack data on most phenotypic traits to conduct meaningful evaluations. Reptiles are important members of ecosystems worldwide, and with over 6,600 species, lizards make up more than 60% of all reptiles (Uetz, 2020). Yet, our synthesis shows that only 22 lizard species have been studied in the context of urbanization. Although not all lizard species filter into urban habitats (e.g., Shea, 2010), the paucity of studies on a variety of species is likely not due to lack of availability. An additional limitation in synthesizing data across urbanized areas is the differences in criteria used to define what is "urban." Indeed, some studies were conducted in small villages whereas others were in large cities. The inclusion of urban locality as a random effect displayed high variance in the meta-regression model ($I^2_{[\text{locality}]} = 59.9\%$), suggesting that such differences among urban environments are important at influencing phenotypic responses. Finally, we

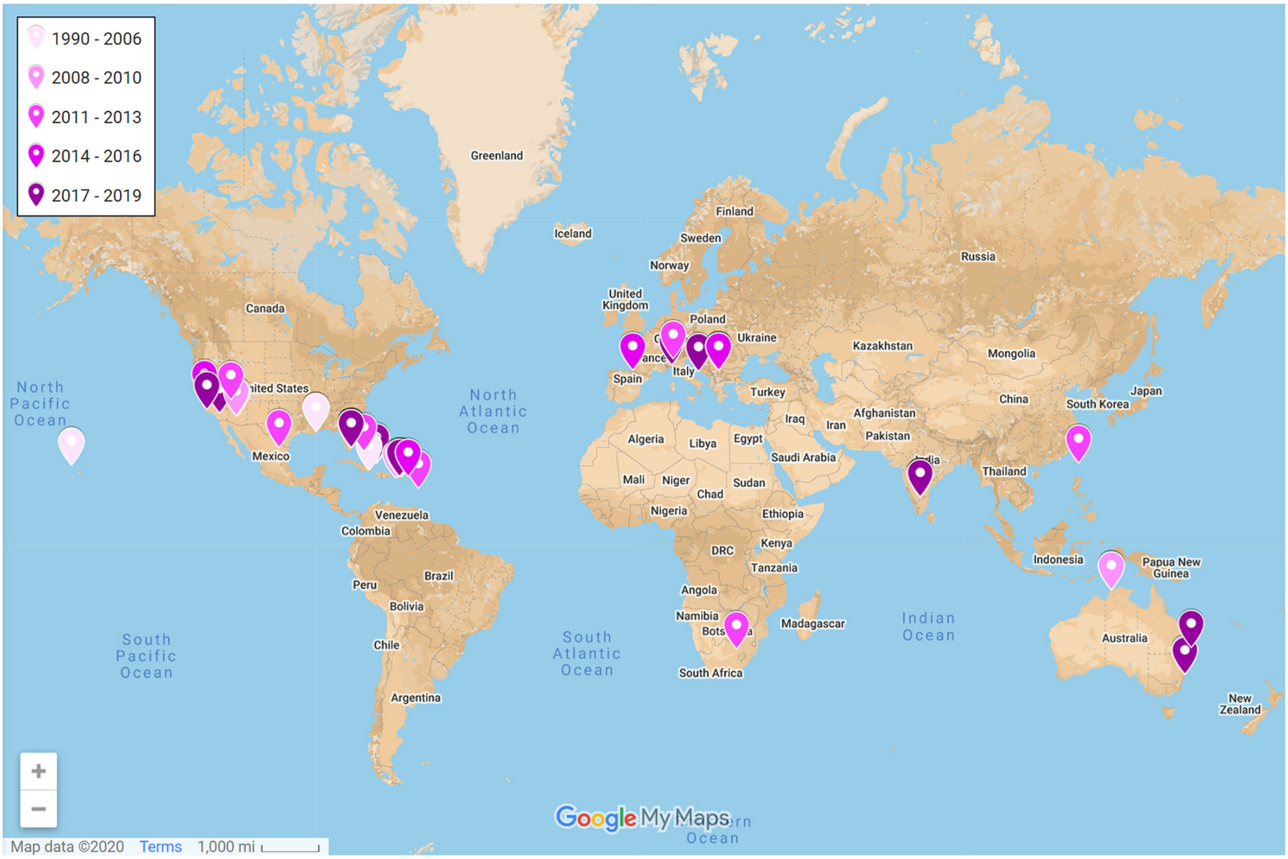

FIGURE 4 | Geographic locations of studies on urban lizards included in the qualitative synthesis ($N = 54$). Points represent averaged centroids of urban replicate localities. Tags are colored by publication year; darker tags are more recent (range: 1990–2019). A full interactive evidence atlas can be found here: https://www.google.com/maps/d/edit?mid=1SAgOD-kWvbQfOXB9_Om-vQVAgk1udo8c&usp=sharing.

also found that most studies are conducted in a single year and so we also lack data on seasonal or yearly variations in traits or information on how traits might change over time. In all, more research will be needed to produce meaningful generalizations on the effects of urbanization on this diverse group of vertebrates.

The most robust finding from our quantitative analysis is that urban lizards are larger than their non-urban counterparts. This finding remained robust even when accounting for sex and when removing data associated with anoles (family *Dactyloidae*). Our study therefore adds to the growing literature on shifts in animal body size associated with urbanization. Nonetheless, lizards do not respond in the same way as other animal groups. Almost all studies on urban invertebrates show a decline in body size with urbanization (Ulrich et al., 2008; Brans et al., 2017; Merckx et al., 2018; Eggenberger et al., 2019) and this is thought to be driven by the urban heat island effect because animals with larger surface area to volume ratios are favored under warmer conditions (Scheffers et al., 2016). Birds show a similar pattern with a general decrease in body size with urbanization (Kark et al., 2007; Liker et al., 2008; Meillère et al., 2015, 2017; Biard et al., 2017), although not all studies support this (Evans et al., 2009). Although these smaller body sizes could be due to nutritional deficits (Meillère et al., 2017), one study found that the difference in body size between urban and rural birds persisted even under laboratory conditions with access to the same amount of food (Liker et al., 2008). Thus, this could also be an evolutionary response to urban heat islands. Urban lizards have been found to physiologically respond to the increased temperature of cities (Campbell-Staton et al., 2020), but our results on body size contradict the findings on other urban taxa. Our results are more in line with those for mammals: larger species (Santini et al., 2019) or moderately-sized species (Bateman and Fleming, 2012) are more likely to be found within urban habitats. For mammals, body size promotes dispersal and ranging abilities, and so larger species do better in cities because they can access widely spaced habitat patches (Santini et al., 2013). However, most lizards do not have large home ranges like mammals, and it is unlikely that an increase in dispersal due to larger body size would benefit them in urban habitats. Thus, we find that different animal taxa respond in different ways and perhaps for different reasons. This information will be useful for holistically managing or conserving urban ecological communities.

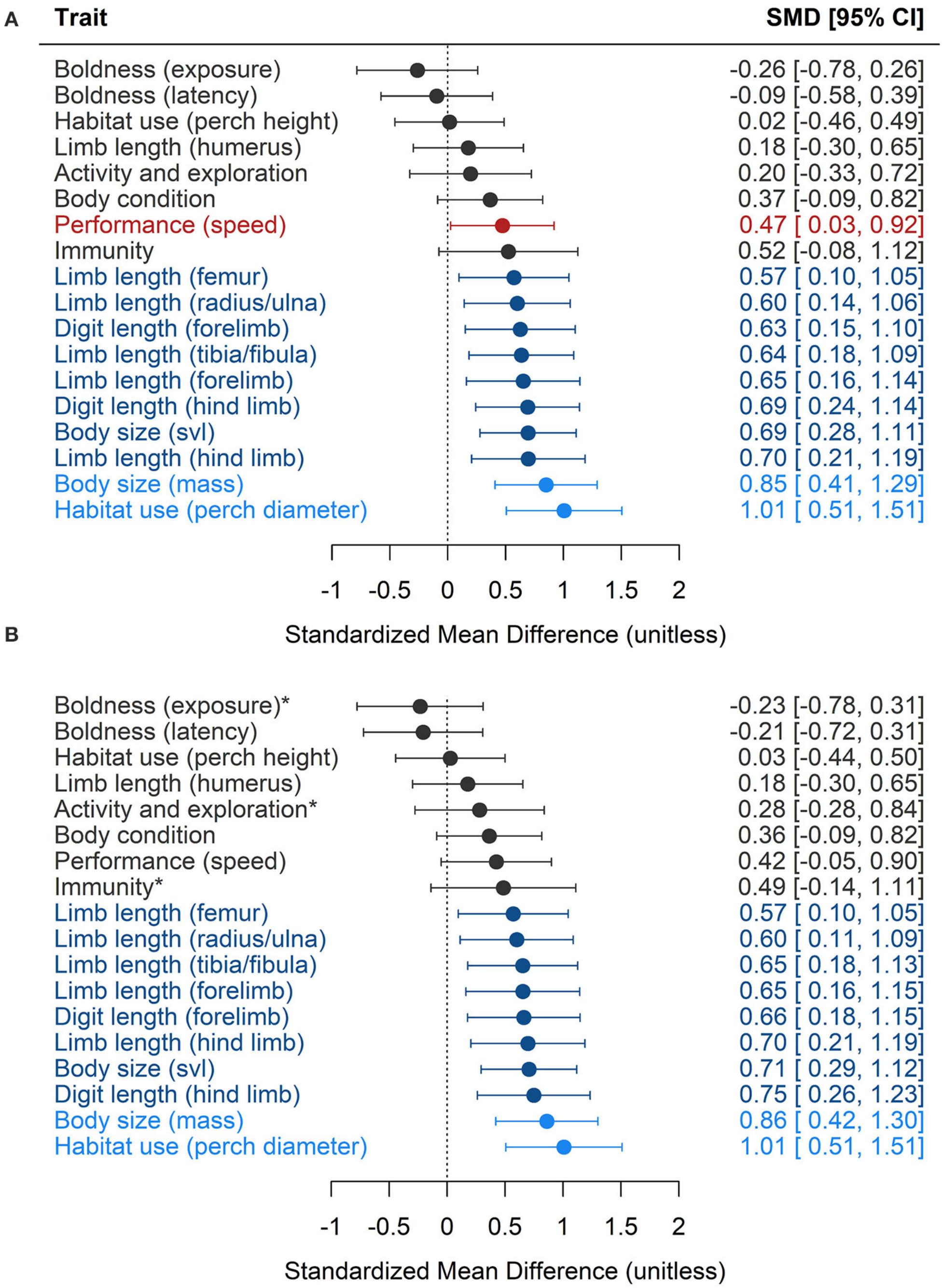

FIGURE 5 | The effect of urbanization on lizard phenotypic traits in **(A)** the full model with all recorded effect sizes (*n* = 348), and **(B)** the reduced model with pseudoreplicated effect sizes removed (*n* = 274). Significant results are shown in blue (dark blue indicating medium effects, SMD > 0.5, and light blue indicating large effects, SMD > 0.8) and error bars represent 95% confidence intervals. One trait, running performance, is highlighted in red as it reached significance in the full model, but not in the reduced model. Traits in the reduced model that failed to meet the minimum sample size of 10 effect sizes are indicated with asterisks. Snout-vent-length, a measure of lizard body length, is abbreviated to svl.

An increase in lizard body size with urbanization could be the result of multiple non-mutually exclusive hypotheses, yet few studies have specifically tested these. First, urban lizards might have access to higher quality, more abundant, and/or more stable resources. This has been shown for other urban vertebrates such as birds, which benefit from supplemental feeding by humans through bird feeders (Robb et al., 2008). Although, it is unlikely that most humans are actively providing food for lizards as most consume invertebrate prey. However, lizard prey could become stable, abundant and concentrated

TABLE 1 | Summaries of the meta–regression models with significant results shown in bold (*n*, number of effect sizes; *k*, number of lizard species).

		Full model (*N* = 348)						**Reduced model (*N* = 274)**					
Moderator	**Levels**	***n***	***k***	**Estimate**	***SE***	**Lower CI (95%)**	**Upper CI (95%)**	***n***	***k***	**Estimate**	***SE***	**Lower CI (95%)**	**Upper CI (95%)**
Trait	Activity and exploration	11	5	0.198	0.268	−0.328	0.723	8	5	0.281	0.285	−0.277	0.839
	Body condition	21	6	0.367	0.232	−0.088	0.822	21	6	0.365	0.231	−0.089	0.818
	Body size (mass)	23	6	**0.850**	**0.225**	**0.409**	**1.292**	23	6	**0.861**	**0.225**	**0.420**	**1.302**
	Body size (svl)	40	10	**0.695**	**0.212**	**0.279**	**1.111**	40	10	**0.707**	**0.211**	**0.294**	**1.119**
	Boldness (exposure)	11	6	−0.263	0.266	−0.785	0.260	9	6	−0.233	0.278	−0.777	0.311
	Boldness (latency)	23	4	−0.094	0.246	−0.576	0.387	13	4	−0.207	0.262	−0.721	0.308
	Digit length (forelimb)	15	3	**0.627**	**0.242**	**0.152**	**1.102**	13	3	**0.662**	**0.248**	**0.176**	**1.148**
	Digit length (hind limb)	26	3	**0.691**	**0.229**	**0.243**	**1.139**	13	3	**0.748**	**0.248**	**0.262**	**1.235**
	Habitat use (perch diameter)	10	3	**1.006**	**0.255**	**0.507**	**1.505**	10	3	**1.008**	**0.256**	**0.506**	**1.509**
	Habitat use (perch height)	14	4	0.016	0.241	−0.456	0.487	14	4	0.028	0.241	−0.444	0.501
	Immunity	10	5	0.524	0.306	−0.076	1.124	8	5	0.486	0.319	−0.139	1.112
	Limb length (femur)	15	4	**0.572**	**0.242**	**0.097**	**1.047**	15	4	**0.571**	**0.242**	**0.096**	**1.046**
	Limb length (forelimb)	12	3	**0.653**	**0.250**	**0.162**	**1.143**	12	3	**0.654**	**0.251**	**0.162**	**1.145**
	Limb length (hind limb)	12	3	**0.697**	**0.250**	**0.206**	**1.188**	12	3	**0.697**	**0.251**	**0.205**	**1.189**
	Limb length (humerus)	15	4	0.178	0.243	−0.298	0.654	15	4	0.179	0.243	−0.297	0.654
	Limb length (radius/ulna)	22	3	**0.601**	**0.234**	**0.143**	**1.059**	13	3	**0.601**	**0.249**	**0.112**	**1.089**
	Limb length (tibia/fibula)	24	4	**0.637**	**0.231**	**0.185**	**1.090**	15	4	**0.653**	**0.242**	**0.178**	**1.128**
	Performance (speed)	44	5	**0.473**	**0.228**	**0.026**	**0.919**	20	5	0.425	0.243	−0.051	0.901

Snout-vent-length, a measure of lizard body length, is abbreviated to svl. Data sets used for each model can be found in ***Supplementary Table 3*** *(full data set) and* ***Supplementary Table 4*** *(reduced data set).*

around anthropogenic sources such as areas of human rubbish (Gross, 2015) or artificial lights (Perry et al., 2008), both of which attract different types of invertebrates. Iglesias et al. (2012) found support, through quantification of invertebrate prey abundance, for more stable resource availability in urban areas compared to natural areas. They also found that urban *Lophognathus temporalis* lizard populations consumed more food, on average, than non-urban populations. Changes in the types and diversity of available prey could also contribute to increased body size with urbanization. Indeed, studies show differential diets between urban and non-urban lizard populations with some species experiencing an increase in dietary breath (de Carvalho et al., 2007), while others showing a narrowing of diet (Balakrishna et al., 2016). Third, lizards might spend more time foraging in urban habitats because of a reduction in overall predation risk that occurs with urbanization (Eötvös et al., 2018). Based on risk-allocation theory, lizards can devote more time and energy toward foraging when predation risk is lower (Lima and Dill, 1990; Ydenberg, 2010). Conversely, a shift toward larger body sizes might be an evolutionary response to escape predation. Individuals of larger size are generally less susceptible to predation than smaller individuals because of enhanced locomotor performance (Irschick, 2000), greater bite force (defensive retaliation; Herrel and O'Reilly, 2006), or because they are released from being prey for small-bodied predators (Vitt, 2000). Cats have been shown to be a major predator of herpetofauna in urban areas (Loyd et al., 2013; Kitts-Morgan, 2015), and larger lizards might be better at escaping cat predation for the above-mentioned reasons. In all, these hypotheses remain untested and therefore, our meta-analysis indicates multiple directions for future research.

We also found that urban lizards use wide perches, most likely because they are climbing on human-made structures such as buildings and walls. They also tend to have longer limbs and digits than their non-urban counterparts. Previous studies have shown that longer limbs and toes, at least in anoles, enhance performance on broad and smooth substrates, such as concrete (Kolbe et al., 2016; Winchell et al., 2018). However, the increase in limb and toe lengths that we found might also be a result of increased body size as most of the means in our database were not scaled to body size (as reported by the authors). Also, these three phenotypic traits (perch width, limb lengths, and digit lengths) were measured mainly within a single lizard family, *Dactyloidae*, on just a few species of arboreal anoles. Because of this, we could not perform subgroup sensitivity analyses to determine the robustness of these findings beyond this taxonomic group or to determine whether non-arboreal lizards respond in similar ways. Thus, we are hesitant to make broad generalizations regarding the effect of urbanization on these traits. It remains to be determined how lizard species from other families will respond. For example, a study on non-anole lizards (*Sceloporus occidentalis*) in our database found a reduction in limb lengths with urbanization (Sparkman et al., 2018). A more recent study, not included in our analysis because it was published after our literature search, also found the same pattern of reduced limb and toe lengths in urban populations of *S. occidentalis* (Putman et al., 2019a). *Sceloporus occidentalis* is less arboreal than most anoles and this may explain these conflicting results. In all, our qualitative synthesis and meta-analysis indicate that research on lizard species outside of *Dactyloidae*, and on lizard taxa that vary in life history and in ecomorphological characteristics, will be valuable in making generalizable predictions, which we are unable to do at this time based on the current state of the literature.

Other than habitat use (perch width), we failed to find consistent shifts in behavioral responses with urbanization. For the two personality traits, activity/exploration and boldness, we did not detect a general effect of urbanization, even though urban populations of other taxa display consistent shifts (Lowry et al., 2013; Sol et al., 2013). Previous research and a global quantitative synthesis have shown urban animals to be more bold in terms of escape responses such as flight initiation distance (FID) (Møller et al., 2015; Samia et al., 2015). We had an inadequate sample size to test for this in our data set; only a handful of studies have compared FID between urban and non-urban lizard populations. It is possible that we did not find patterns as strong as those for morphological traits because behaviors are more difficult to quantify in a standardized manner across studies. Even though we attempted to group behaviors based on assays used for quantification, such as latency to respond to stimuli or willingness to be exposed, other factors could influence these traits such as whether traits were measured in the lab or field, lizard body temperature, and even the season or time of testing. Morphological traits, such as body length or limb length, are less sensitive to such factors. Clearly more research is needed to determine whether boldness, exploration, activity, sociability, or other personality traits generally associate with urbanization in lizards.

Our meta-analysis reveals various phenotypic shifts in lizards due to urbanization, yet we are unable to determine whether these are associated with underlying genetic changes. A few studies assessed the heritability of traits through common garden rearing of offspring from urban and natural habitats (Winchell et al., 2016; Hall and Warner, 2017; Tiatragul et al., 2017). Other studies (not included in our analysis) have shown strong morphological and genetic differentiation among lizard populations living in urban parks in a single city (Littleford-Colquhoun et al., 2017), and tolerance of higher temperatures (in response to the urban heat island effect) in urban *Anolis cristatellus* populations has been linked to a single gene polymorphism (Campbell-Staton et al., 2020). Together, these studies provide support for rapid evolution of traits due to urbanization, a phenomenon that appears to induce greater rates of phenotypic change than other forms of human disturbance (Alberti et al., 2017). More studies are needed though to determine the exact mechanisms driving phenotypic change as shifts could also be due to phenotypic plasticity or differential sorting of individuals into urban habitats. This information is important because populations could have limits to plasticity (van Baaren and Candolin, 2018) and sorting of individuals could reduce genetic diversity, limiting urban populations' abilities to respond to additional environmental disturbances (Barrett and Schluter, 2008).

Finally, we also lack support for whether the phenotypic shifts associated with urban living improve fitness within these anthropogenic habitats. It is possible that larger body sizes correlate with larger clutch or egg sizes (Dunham and Miles, 1985). Yet, even though we have documented some shifts in lizard phenotypes due to urbanization, these responses can also be maladaptive, creating evolutionary and ecological traps (Robertson et al., 2013; Hale and Swearer, 2016), or they could be insufficient to overcome novel selection pressures leading to extirpation of populations over time (Sinervo et al., 2010). A few species in our dataset are invasive at the locations where they were studied (e.g., *Anolis cristatellus* and *A. sagrei*), and these species might have higher fitness in urban areas because their evolutionary histories are often associated with humans and anthropogenic habitats (Hufbauer et al., 2012). We did not test for the effects of invasive status in our model, but further studies on this would improve our understanding of interspecific differences in responses to urbanization. Hall and Warner (2017) found that the large body size of urban invasive female anoles was associated with higher body condition and fecundity as these females starting laying eggs earlier in the season than females from non-urban habitats. Lucas and French (2012) also found urban populations of *Uta stansburiana* had higher fecundity (larger clutches and eggs) than non-urban populations, but this was at the cost of reduced survival. These studies provide partial support that lizards are responding adaptively to urbanization, yet Tiatragul et al. (2017) found that urban anole embryos were not more robust to urban thermal environments than non-urban embryos, suggesting a lack of adaptation. In sum, we will need much more research to determine the fitness impacts of phenotypic responses, which could set priorities for conservation management of urban populations.

CONCLUSIONS

Our synthesis of the current urban lizard literature reveals large data gaps in various areas including geographic, taxonomic, and phenotypic extent. Even so, our meta-analysis reveals a robust finding of an increase in lizard body size with urbanization, although we still do not know the mechanism(s) driving this phenotypic shift. We demonstrate that this response differs from that of other urban animal groups, namely invertebrates and birds. Further research is needed to understand whether documented shifts in phenotypic traits are adaptive and/or great enough to withstand the pressures of urban life. In sum, our study provides a path forward for future studies and contributes to the growing literature on animal responses to rapid human-induced habitat change.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Materials**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

BP conceived of the study and performed the literature search and study selection process. BP and ZT extracted the data from studies. ZT conducted the qualitative synthesis and BP conducted the phylogenetic meta-analysis. Both authors contributed to writing the article.

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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.2020.580745/full#supplementary-material

REFERENCES

Alberti, M., Correa, C., Marzluff, J. M., Hendry, A. P., Palkovacs, E. P., Gotanda, K. M., et al. (2017). Global urban signatures of phenotypic change in animal and plant populations. *Proc. Natl. Acad. Sci. U.S.A.* 114, 8951–8956. doi: 10.1073/pnas.1606034114

Angilletta, M. J., Wilson, R. S., Niehaus, A. C., Sears, M. W., Navas, C. A., and Ribeiro, P. L. (2007). Urban physiology: city ants possess high heat tolerance. *PLoS ONE* 2:e258. doi: 10.1371/journal.pone.0000258

Balakrishna, S., Batabyal, A., and Thaker, M. (2016). Dining in the city: dietary shifts in Indian rock agamas across an urban-rural landscape. *J. Herpetol.* 50, 423–428. doi: 10.1670/14-073

Barrett, R. D. H., and Schluter, D. (2008). Adaptation from standing genetic variation. *Trends Ecol. Evol.* 23, 38–44. doi: 10.1016/j.tree.2007.09.008

Bateman, P. W., and Fleming, P. A. (2012). Big city life: carnivores in urban environments. *J. Zool.* 287, 1–23. doi: 10.1111/j.1469-7998.2011.00887.x

Benítez-López, A., Alkemade, R., and Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biol. Conserv.* 143, 1307–1316. doi: 10.1016/j.biocon.2010.02.009

Berthouly-Salazar, C., van Rensburg, B. J., Le Roux, J. J., van Vuuren, B. J., and Hui, C. (2012). Spatial sorting drives morphological variation in the invasive bird, *Acridotheris tristis*. *PLoS ONE* 7:e38145. doi: 10.1371/journal.pone.0038145

Biard, C., Brischoux, F., Meillère, A., Michaud, B., Nivière, M., Ruault, S., et al. (2017). Growing in cities: an urban penalty for wild birds? *A study of phenotypic differences between urban and rural great tit chicks (Parus major). Front. Ecol. Evol.* 5:79. doi: 10.3389/fevo.2017.00079

Biermann, F., Bai, X., Bondre, N., Broadgate, W., Arthur Chen, C. T., Dube, O. P., et al. (2016). Down to earth: contextualizing the anthropocene. *Glob. Environ. Change* 39, 341–350. doi: 10.1016/j.gloenvcha.2015.11.004

Borenstein, M., Hedges, L. V., Higgins, J. P. T., and Rothstein, H. R. (2009). *Introduction to Meta-Analysis. Chichester: John Wiley & Sons, Ltd.*

Brans, K. I., Jansen, M., Vanoverbeke, J., Tüzün, N., Stoks, R., and De Meester, L. (2017). The heat is on: genetic adaptation to urbanization mediated by thermal tolerance and body size. *Glob. Chang. Biol.* 23, 5218–5227. doi: 10.1111/gcb.13784

Camargo, A., Sinervo, B., and Sites, J. W. (2010). Lizards as model organisms for linking phylogeographic and speciation studies. *Mol. Ecol.* 19, 3250–3270. doi: 10.1111/j.1365-294X.2010.04722.x

Campbell-Staton, S. C., Winchell, K. M., Rochette, N. C., Fredette, J., Maayan, I., Schweizer, R. M., et al. (2020). Parallel selection on thermal physiology facilitates repeated adaptation of city lizards to urban heat islands. *Nat. Ecol. Evol.* 4, 652–658. doi: 10.1038/s41559-020-1131-8

Chamberlain, D. E., Cannon, A. R., Toms, M. P., Leech, D. I., Hatchwell, B. J., and Gaston, K. J. (2009). Avian productivity in urban landscapes: a review and meta-analysis. *Ibis* 151, 1–18. doi: 10.1111/j.1474-919X.2008.00899.x

Croci, S., Butet, A., and Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits? *Condor* 110, 223–240. doi: 10.1525/cond.2008.8409

de Carvalho, A. L. G., da Silva, H. R., de Araújo, A. F. B., Alves-Silva, R., and da Silva-Leite, R. R. (2007). Feeding ecology of *Tropidurus torquatus* (Wied) (*Squamata*, *Tropiduridae*) in two areas with different degrees of conservation in Marambaia Island, Rio de Janeiro, Southeastern Brazil. *Rev. Bras. Zool.* 24, 222–227. doi: 10.1590/S0101-81752007000100029

de Miranda, E. B. P. (2017). The plight of reptiles as ecological actors in the tropicss. *Front. Ecol. Evol.* 5:159. doi: 10.3389/fevo.2017.00159

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., and Collen, B. (2014). Defaunation in the anthropocene. *Science* 345, 401–406. doi: 10.1126/science.1251817

Dobbs, C., Nitschke, C., and Kendal, D. (2017). Assessing the drivers shaping global patterns of urban vegetation landscape structure. *Sci. Total Environ.* 592, 171–177. doi: 10.1016/j.scitotenv.2017.03.058

Doherty, T. S., Balouch, S., Bell, K., Burns, T. J., Feldman, A., Fist, C., et al. (2020). Reptile responses to anthropogenic habitat modification: a global meta-analysis. *Glob. Ecol. Biogeogr.* 29, 1265–1279. doi: 10.1111/geb.13091

Dunham, A. E., and Miles, D. B. (1985). Patterns of covariation in life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. *Am. Nat.* 126, 231–257. doi: 10.1086/284411

Eggenberger, H., Frey, D., Pellissier, L., Ghazoul, J., Fontana, S., and Moretti, M. (2019). Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. *J. Anim. Ecol.* 88, 1522–1533. doi: 10.1111/1365-2656.13051

Eötvös, C. B., Magura, T., and Lövei, G. L. (2018). A meta-analysis indicates reduced predation pressure with increasing urbanization. *Landsc. Urban Plan.* 180, 54–59. doi: 10.1016/j.landurbplan.2018.08.010

Evans, K. L., Chamberlain, D. E., Hatchwell, B. J., Gregory, R. D., and Gaston, K. J. (2011). What makes an urban bird? *Glob. Chang. Biol.* 17, 32–44. doi: 10.1111/j.1365-2486.2010.02247.x

Evans, K. L., Gaston, K. J., Sharp, S. P., Mcgowan, A., and Hatchwell, B. J. (2009). The effect of urbanisation on avian morphology and latitudinal gradients in body size. *Oikos* 118, 251–259. doi: 10.1111/j.1600-0706.2008.17092.x

French, S. S., Webb, A. C., Hudson, S. B., and Virgin, E. E. (2018). Town and country reptiles: a review of reptilian responses to urbanization. *Integr. Comp. Biol.* 58, 948–966. doi: 10.1093/icb/icy052

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., and Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science* 360, 1232–1235. doi: 10.1126/science.aar7121

Giraudeau, M., Nolan, P. M., Black, C. E., Earl, S. R., Hasegawa, M., and McGraw, K. J. (2014). Song characteristics track bill morphology along a gradient of urbanization in house finches (*Haemorhous mexicanus*). *Front. Zool.* 11:83. doi: 10.1186/s12983-014-0083-8

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., et al. (2008). Global change and the ecology of cities. *Science* 319, 756–760. doi: 10.1126/science.1150195

Gross, S. D. (2015). *Carrion-associated arthropods in rural and urban environments*. (Dissertation), Purdue University, West Lafayette, IN (USA).

Hale, R., and Swearer, S. E. (2016). Ecological traps: current evidence and future directions. *Proc. R. Soc. London B.* 283:20152647. doi: 10.1098/rspb.2015.2647

Hall, J. M., and Warner, D. A. (2017). Body size and reproduction of a non-native lizard are enhanced in an urban environment. *Biol. J. Linn. Soc.* 122, 860–871. doi: 10.1093/biolinnean/blx109

Hamer, A. J., and McDonnell, M. J. (2008). Amphibian ecology and conservation in the urbanising world: a review. *Biol. Conserv.* 141, 2432–2449. doi: 10.1016/j.biocon.2008.07.020

Hedges, L. V. (1981). Distribution theory for Glass's estimator of effect size and related estimators. *J. Educ. Stat.* 6, 107–128. doi: 10.3102/10769986006002107

Herrel, A., and O'Reilly, J. C. (2006). Ontogenetic scaling of bite force in lizards and turtles. *Physiol. Biochem. Zool.* 79, 31–42. doi: 10.1086/498193

Hufbauer, R. A., Facon, B., Ravigne, V., Turgeon, J., Foucaud, J., et al. (2012). Anthropogenically induced adaptation to invade (AIAI): contemporary adaptation to human-altered habitats within the native range can promote invasions. *Evol. Appl.* 5, 89–101. doi: 10.1111/j.1752-4571.2011.00211.x

Hulley, M. E. (2012). "The urban heat island effect: Causes and potential solutions," in *Metropolitan Sustainability*, ed *F. Zeman (Cambridge: Woodhead Publishing)*, 79–98.

Iglesias, S., Tracy, C., Bedford, G., and Christian, K. (2012). Habitat differences in body size and shape of the Australian agamid lizard, *Lophognathus temporalis*. *J. Herpetol.* 46, 297–303. doi: 10.1670/11-084

Irschick, D. J. (2000). Effects of behaviour and ontogeny on the locomotor performance of a West Indian lizard, *Anolis lineatopus*. *Funct. Ecol.* 14, 438–444. doi: 10.1046/j.1365-2435.2000.00447.x

Jessop, T. S., Ariefiandy, A., Forsyth, D. M., Purwandana, D., White, C. R., Benu, Y. J., et al. (2020). Komodo dragons are not ecological analogs of apex mammalian predators. *Ecology* 101:e02970. doi: 10.1002/ecy.2970

Johnson, M. T. J., and Munshi-South, J. (2017). Evolution of life in urban environments. *Science* 358:eaam8327. doi: 10.1126/science.aam8327

Kark, S., Iwaniuk, A., Schalimtzek, A., and Banker, E. (2007). Living in the city: can anyone become an "urban exploiter"? *J. Biogeogr.* 34, 638–651. doi: 10.1111/j.1365-2699.2006.01638.x

Kettel, E. F., Gentle, L. K., Quinn, J. L., and Yarnell, R. W. (2018). The breeding performance of raptors in urban landscapes: a review and meta-analysis. *J. Ornithol.* 159, 1–18. doi: 10.1007/s10336-017-1497-9

Kinnison, M. T., and Hendry, A. P. (2001). The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* 112–113, 145–164. doi: 10.1007/978-94-010-0585-2_10

Kitts-Morgan, S. E. (2015). Sustainable ecosystems: domestic cats and their effect on wildlife populations. *J. Anim. Sci.* 93, 848–859. doi: 10.2527/jas.2014-8557

Kolbe, J. J., Battles, A. C., and Aviles-Rodriguez, K. J. (2016). City slickers: poor performance does not deter *Anolis* lizards from using artificial substrates in human-modified habitats. *Funct. Ecol.* 30, 1418–1429. doi: 10.1111/1365-2435.12607

Konstantopoulos, S. (2011). Fixed effects and variance components estimation in three-level meta-analysis. *Res. Synth. Methods.* 2, 61–76. doi: 10.1002/jrsm.35

LaMontagne, J. M., Kilgour, R. J., Anderson, E. C., and Magle, S. (2015). Tree cavity availability across forest, park, and residential habitats in a highly urban area. *Urban Ecosyst.* 18, 151–167. doi: 10.1007/s11252-014-0383-y

Lapiedra, O. (2018). Urban behavioral ecology: lessons from *Anolis* lizards. *Integr. Comp. Biol.* 58, 939–947. doi: 10.1093/icb/icy109

Lapiedra, O., Chejanovski, Z., and Kolbe, J. J. (2017). Urbanization and biological invasion shape animal personalities. *Glob. Chang. Biol.* 23, 592–603. doi: 10.1111/gcb.13395

Lewis, S. L., and Maslin, M. A. (2015). Defining the anthropocene. *Nature* 519, 171–180. doi: 10.1038/nature14258

Liker, A., Papp, Z., Bókony, V., and Lendvai, Á. Z. (2008). Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. *J. Anim. Ecol.* 77, 789–795. doi: 10.1111/j.1365-2656.2008.01402.x

Lima, S. L., and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640. doi: 10.1139/z90-092

Littleford-Colquhoun, B. L., Clemente, C., Whiting, M. J., Ortiz-Barrientos, D., and Frere, C. H. (2017). Archipelagos of the Anthropocene: rapid and extensive differentiation of native terrestrial vertebrates in a single metropolis. *Mol. Ecol.* 26, 2466–2481. doi: 10.1111/mec.14042

Łopucki, R., and Kitowski, I. (2017). How small cities affect the biodiversity of ground-dwelling mammals and the relevance of this knowledge in planning urban land expansion in terms of urban wildlife. *Urban Ecosyst.* 20, 933–943. doi: 10.1007/s11252-016-0637-y

Lowry, H., Lill, A., and Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549. doi: 10.1111/brv.12012

Loyd, K. A. T., Hernandez, S. M., Carroll, J. P., Abernathy, K. J., and Marshall, G. J. (2013). Quantifying free-roaming domestic cat predation using animal-borne video cameras. *Biol. Conserv.* 160, 183–189. doi: 10.1016/j.biocon.2013.01.008

Lucas, L. D., and French, S. S. (2012). Stress-induced tradeoffs in a free-living lizard across a variable landscape: consequences for individuals and populations. *PLoS ONE* 7:e49895. doi: 10.1371/journal.pone.0049895

Mallen-Cooper, M., Nakagawa, S., and Eldridge, D. J. (2019). Global meta-analysis of soil-disturbing vertebrates reveals strong effects on ecosystem patterns and processes. *Glob. Ecol. Biogeogr.* 28, 661–679. doi: 10.1111/geb.12877

Martin, P. R., and Bonier, F. (2018). Species interactions limit the occurrence of urban-adapted birds in cities. *Proc. Natl. Acad. Sci. U.S.A.* 115, E11495–E11504. doi: 10.1073/pnas.1809317115

McDonnell, M. J., and Hahs, A. K. (2015). Adaptation and adaptedness of organisms to urban environments. *Annu. Rev. Ecol. Evol. Syst.* 46, 261–280. doi: 10.1146/annurev-ecolsys-112414-054258

McKinney, M. L. (2008). Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst.* 11, 161–176. doi: 10.1007/s11252-007-0045-4

Meillère, A., Brischoux, F., Henry, P. Y., Michaud, B., Garcin, R., and Angelier, F. (2017). Growing in a city: consequences on body size and plumage quality in an urban dweller, the house sparrow (*Passer domesticus*). *Landsc. Urban Plan.* 160, 127–138. doi: 10.1016/j.landurbplan.2016.12.014

Meillère, A., Brischoux, F., Parenteau, C., and Angelier, F. (2015). Influence of urbanization on body size, condition, and physiology in an urban exploiter: a multi-component approach. *PLoS ONE* 10:e0135685. doi: 10.1371/journal.pone.0135685

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L. F., Backeljau, T., Bonte, D., et al. (2018). Body-size shifts in aquatic and terrestrial urban communities. *Nature* 558, 113–116. doi: 10.1038/s41586-018-0140-0

Miller, C. R., Latimer, C. E., and Zuckerberg, B. (2018). Bill size variation in northern cardinals associated with anthropogenic drivers across North America. *Ecol. Evol.* 8, 4841–4851. doi: 10.1002/ece3.4038

Miranda, A. C., Schielzeth, H., Sonntag, T., and Partecke, J. (2013). Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Glob. Chang. Biol.* 19, 2634–2644. doi: 10.1111/gcb.12258

Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., Altman, D., Antes, G., et al. (2009). Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS Med.* 6:e1000097. doi: 10.1371/journal.pmed.1000097

Møller, A. P. (2009). Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the western palearctic. *Oecologia* 159, 849–858. doi: 10.1007/s00442-008-1259-8

Møller, A. P., Tryjanowski, P., Diaz, M., Kwiecinski, Z., Indykiewicz, P., Mitrus, C., et al. (2015). Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behav. Ecol.* 26, 861–865. doi: 10.1093/beheco/arv024

Nakagawa, S., Noble, D. W. A., Senior, A. M., and Lagisz, M. (2017). Meta-evaluation of meta-analysis: Ten appraisal questions for biologists. *BMC Biol.* 15:18. doi: 10.1186/s12915-017-0357-7

Nakagawa, S., and Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evol. Ecol.* 26, 1253–1274. doi: 10.1007/s10682-012-9555-5

Nelson, J. A., Atzori, F., and Gastrich, K. R. (2015). Repeatability and phenotypic plasticity of fish swimming performance across a gradient of urbanization. *Environ. Biol. Fishes* 98, 1431–1447. doi: 10.1007/s10641-014-0369-x

Nowak, E. M., Theimer, T. C., and Schuett, G. W. (2008). Functional and numerical responses of predators: where do vipers fit in the traditional paradigms? *Biol. Rev. Camb. Philos. Soc.* 83, 601–620. doi: 10.1111/j.1469-185X.2008.00056.x

Ordeñana, M. A., Crooks, K. R., Boydston, E. E., Fisher, R. N., Lyren, L. M., Siudyla, S., et al. (2010). Effects of urbanization on carnivore species distribution and richness. *J. Mammal.* 91, 1322–1331. doi: 10.1644/09-MAMM-A-312.1

Perry, G., Buchanan, B. W., Fisher, R. N., Salmon, M., and Wise, S. E. (2008). "Effects of night lighting on urban reptiles and amphibians," in *Urban Herpetology*, eds *J. C. Mitchell, R. E. Jung Brown, and B. Bartholomew (Society for the Study of Amphibians and Reptiles)* (Salt Lake City), 239–256.

Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., et al. (2017). Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Glob. Chang. Biol.* 23, 2554–2564. doi: 10.1111/gcb.13606

Putman, B. J., Gasca, M., Blumstein, D. T., and Pauly, G. B. (2019a). Downsizing for downtown : limb lengths, toe lengths, and scale counts decrease with urbanization in western fence lizards (*Sceloporus occidentalis*). *Urban Ecosyst.* 22, 1071–1081. doi: 10.1007/s11252-019-00889-z

Putman, B. J., Samia, D. S. M., Cooper, W. E., and Blumstein, D. T. (2019b). "Impact of human-induced environmental changes on lizard behavior: insights from urbanization," in *Behavior of Lizards*, eds *V. L. Bels and A. Russell (Boca Raton: CRC Press),* 375–396.

Pyron, R., Burbrink, F., and Wiens, J. (2013). A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evol. Biol.* 13:93. doi: 10.1186/1471-2148-13-93

Robb, G. N., McDonald, R. A., Chamberlain, D. E., and Bearhop, S. (2008). Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.* 6, 476–484. doi: 10.1890/060152

Robertson, B. A., Rehage, J. S., and Sih, A. (2013). Ecological novelty and the emergence of evolutionary traps. *Trends Ecol. Evol.* 28, 552–560. doi: 10.1016/j.tree.2013.04.004

Roca, I. T., Desrochers, L., Giacomazzo, M., Bertolo, A., Bolduc, P., Deschesnes, R., et al. (2016). Shifting song frequencies in response to anthropogenic noise: a meta-analysis on birds and anurans. *Behav. Ecol.* 27, 1269–1274. doi: 10.1093/beheco/arw060

Saito, M., and Koike, F. (2013). Distribution of wild mammal assemblages along an urban-rural-forest landscape gradient in warm-temperate East Asia. *PLoS ONE* 8:e65464. doi: 10.1371/journal.pone.0065464

Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F., and Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. *Nat. Commun.* 6:8877. doi: 10.1038/ncomms9877

Santini, L., Di Marcc, M., Visconti, P., Baiserc, D., Boitanl, L., and Rondinini, C. (2013). Ecological correlates of dispersal distance in terrestrial mammals. *Hystrix* 24, 181–186. doi: 10.4404/hystrix-24.2-8746

Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A., and Ancillotto, L. (2019). One strategy does not fit all: determinants of urban adaptation in mammals. *Ecol. Lett.* 22, 365–376. doi: 10.1111/ele.13199

Scheffers, B. R., de Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., et al. (2016). The broad footprint of climate change from genes to biomes to people. *Science* 354:aaf7671. doi: 10.1126/science.aaf7671

Schochet, A. B., Hung, K. L. J., and Holway, D. A. (2016). Bumble bee species exhibit divergent responses to urbanisation in a Southern California landscape. *Ecol. Entomol.* 41, 685–692. doi: 10.1111/een.12343

Seress, G., and Liker, A. (2015). Habitat urbanization and its effects on birds. *Acta Zool. Acad. Sci. Hungaricae* 61, 373–408. doi: 10.17109/AZH.61.4.373.2015

Shea, G. M. (2010). "The suburban terrestrial reptile fauna of Sydney - winners and losers," in *The Natural History of Sydney*, eds D. Lunney, P. Hutchings, and D. *Hochuli (Mosman: Royal Zoological Society of NSW)*, 154–197.

Silva, C. P., Sepúlveda, R. D., and Barbosa, O. (2016). Nonrandom filtering effect on birds: species and guilds response to urbanization. *Ecol. Evol.* 6, 3711–3720. doi: 10.1002/ece3.2144

Sinervo, B., Mendez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., et al. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328, 894–899. doi: 10.1126/science.1184695

Sol, D., Lapiedra, O., and Gonzalez-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Anim. Behav.* 85, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Sparkman, A., Howe, S., Hynes, S., Hobbs, B., and Handal, K. (2018). Parallel behavioral and morphological divergence in fence lizards on two college campuses. *PLoS ONE* 13:e191800. doi: 10.1371/journal.pone.0191800

Symonds, M. R. E., Weston, M. A., van Dongen, W. F. D., Lill, A., Robinson, R. W., and Guay, P. J. (2016). Time since urbanization but not encephalisation is associated with increased tolerance of human proximity in birds. *Front. Ecol. Evol.* 4:117. doi: 10.3389/fevo.2016.00117

Tiatragul, S., Kurniawan, A., Kolbe, J. J., and Warner, D. A. (2017). Embryos of non-native anoles are robust to urban thermal environments. *J. Therm. Biol.* 65, 119–124. doi: 10.1016/j.jtherbio.2017.02.021

Uetz, P. (2020). *Species Statistics August 2019. Available online at: http://www.reptile-database.org/db-info/SpeciesStat.html (accessed July* 5, 2020).

Ulrich, W., Komosiński, K., and Zalewski, M. (2008). Body size and biomass distributions of carrion visiting beetles: do cities host smaller species? *Ecol. Res.* 23, 241–248. doi: 10.1007/s11284-007-0369-9

United Nations (2019). *World Urbanization Prospects: The 2018 Revision.* New York, NY: United Nations.

van Baaren, J., and Candolin, U. (2018). Plasticity in a changing world: behavioural responses to human perturbations. *Curr. Opin. Insect Sci.* 27, 21–25. doi: 10.1016/j.cois.2018.02.003

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor. *J. Stat. Softw.* 36, 1–48. doi: 10.18637/jss.v036.i03

Vitt, L. J. (2000). Ecological consequences of body size in neonatal and small-bodied lizards in the Neotropics. *Herpetol. Monogr.* 14, 388–400. doi: 10.2307/1467053

Voigt, C. C., and Kingston, T. (2015). *Bats in the Anthropocene: Conservation of Bats in a Changing World. New York, NY: Springer*.

Winchell, K. M., Maayan, I., Fredette, J. R., and Revell, L. J. (2018). Linking locomotor performance to morphological shifts in urban lizards. *Proc. R. Soc. B.* 285:20180229. doi: 10.1098/rspb.2018.0229

Winchell, K. M., Reynolds, R. G., Prado-Irwin, S. R., Puente-Rolon, A. R., and Revell, L. J. (2016). Phenotypic shifts in urban areas in the tropical lizard *Anolis cristatellus. Evolution* 70, 1009–1022. doi: 10.1111/evo.12925

Ydenberg, R. (2010). "Decision theory," in *Evolutionary Behavioral Ecology*, eds. D. F. Westneat and C. W. *Fox (New York, NY: Oxford University Press),* 131–147.

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Territory Quality Predicts Avian Vocal Performance Across an Urban-Rural Gradient

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Human activity around the globe is a growing source of selection pressure on animal behavior and communication systems. Some animals can modify their vocalizations to avoid masking from anthropogenic noise. However, such modifications can also affect the salience of these vocalizations in functional contexts such as competition and mate choice. Such is the case in the well-studied Nuttall's white-crowned sparrow (*Zonotrichia leucophrys nuttalli*), which lives year-round in both urban San Francisco and nearby rural Point Reyes. A performance feature of this species' song is salient in territorial defense, such that higher performance songs elicit stronger responses in simulated territorial intrusions; but songs with lower performance values transmit better in anthropogenic noise. A key question then is whether vocal performance signals male quality and ability to obtain high quality territories in urban populations. We predicted white-crowned sparrows with higher vocal performance will be in better condition and will tend to hold territories with lower noise levels and more species-preferred landscape features. Because white-crowned sparrows are adapted to coastal scrub habitats, we expect high quality territories to contain lower and less dense canopies, less drought, more greenness, and more flat open ground for foraging. To test our predictions, we recorded songs and measured vocal performance and body condition (scaled mass index and fat score) for a set of urban and rural birds ($N = 93$), as well as ambient noise levels on their territories. Remote sensing metrics measured landscape features of territories, such as drought stress (NDWI), greenness (NDVI), mean canopy height, maximum height, leaf area density (understory and canopy), slope, and percent bare ground for a 50 m radius on each male territory. We did not find a correlation between body condition and performance but did find a relationship between noise levels and performance. Further, high performers held territories with lower canopies and less dense vegetation, which are species-preferred landscape features. These findings link together fundamental aspects of sexual selection in that habitat quality and the quality of sexually selected signals appear to be associated: males that have the highest performing songs are defending territories of the highest quality.

Keywords: vocal performance, territory quality, male quality, urban ecology, birdsong, noise pollution

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INTRODUCTION

Urban habitats are an ever-expanding ecosystem with strong selection pressures for wildlife that inhabit them, and the degree of habitat alteration and pollution often determines whether species are urban adapters or urban avoiders (Blair, 1996; Croci et al., 2008; Aronson et al., 2016). Anthropogenic noise, introduced vegetation, exotic predators, increased risk of disease, and smaller patches of suitable habitat all may affect species composition, the population densities of species, and how individual animals behave in an urban environment (Shochat et al., 2010; Aronson et al., 2014; Marzluff, 2017). For species that do persist in urban ecosystems, these selective pressures may compromise their badges of status and sexually selected signals (Swaddle et al., 2015), hampering individuals' abilities to attain and maintain resources that benefit survival and reproductive success. For example, bird song functions in acquisition and defense of breeding territories and attraction of mates (Catchpole and Slater, 2008), and is known to be under selection pressures from urban noise (Slabbekoorn, 2013). However, links between territory quality, individual quality and signal performance have rarely, if ever, been investigated, and to our knowledge never in the context of anthropogenic disturbance.

Obtaining a good territory is the key to higher fitness for most wildlife. Territories with preferred nesting vegetation result in fewer nest failures (Kaiser et al., 2009) and higher fecundity (Pidgeon et al., 2006). Similarly, territories with higher quality food resources result in higher survival rates (Senar et al., 2002). For birds, males without territories, or "floaters," scope out territories by assessing habitat quality features like foraging patches and assessing social context as to whether current territory holders are successful nesters (Pärt et al., 2011). How phenotypic traits, such as song, affect the ability to obtain relatively high quality territories is an outstanding question in behavioral ecology (Andersson, 1994; Catchpole and Slater, 2008). Previous research provides some insight – singing longer, increased age, larger body size, and aggressive behavior are often associated with securing territories (e.g., Yasukawa, 1979; Clarkson, 2007). For example, prothonotary warblers (*Protonotaria citrea*) prefer to nest near wet or flooded areas, and males that sing longer are more likely to attain territories near water; and thus song seems to be used for males to assess the condition of rivals (Clarkson, 2007). Similarly, dominant males in the Paridae family have access to preferred resources (Ekman, 1987; Desrochers, 1989), and male black-capped chickadees (*Poecile atricapillus*) in high quality mature forest signal their competitive ability with more consistent song structure (van Oort et al., 2006; Grava et al., 2012, 2013) and higher song output (van Oort et al., 2007). Blue-black grassquits (*Volatinia jacarina*) that sing more often and consistently have territories with higher seed availability (Manica et al., 2014). However, there are still gaps in our knowledge about how song affects the ability of males to attain and defend high quality territories.

Fewer studies have looked at urban habitat quality (Shochat et al., 2006), and especially not fine-grain habitat characteristics of territories, or how these features might vary with performance of sexually selected signals. Instead of fine-grain metrics like types of cover, studies focus on the rural-urban dichotomy. For example, urban house sparrows (*Passer domesticus*) are smaller and in worse condition than rural birds (Liker et al., 2008), and body size varies with urbanization level (Meillère et al., 2015). Telomere length, which affects life longevity, is also shortened in birds raised in urban conditions (Salmón et al., 2016), but the specific differences between urban and rural conditions (e.g., noise, vegetation) was not examined. Furthermore, none of these aforementioned studies pair song data with habitat data. Only one system to date has investigated whether song traits vary with habitat quality and signaler quality across anthropogenic habitats (Narango and Rodewald, 2016, 2018). In this case, male northern cardinals (*Cardinalis cardinalis*), body size correlates with song speed and length in rural areas but this pattern does not hold across urban and rural locations (Narango and Rodewald, 2018). Additionally, minimum frequency increased with increased understory density, and urban birds sang faster, longer songs (Narango and Rodewald, 2016, 2018). However, song was not related to provisioning ability or number of offspring, although offspring were in worse condition in cities (Narango and Rodewald, 2018). Therefore, there is much that is not understood about the interaction between habitat characteristics, signaling traits, and body condition of individual birds, especially along urban to rural gradients.

How anthropogenic noise affects sexually selected signals used to attain territories has received much attention in recent years. Many avian species adjust their song pitch in noise with long-term, cultural changes, or real-time plasticity shifts in minimum frequency, and thereby avoid masking by high energy, low frequency background noise (Derryberry et al., 2016; LaZerte et al., 2016; Luther et al., 2016 reviewed in Slabbekoorn, 2013). Oftentimes this shift in minimum frequency is associated with reduced bandwidth (Dowling et al., 2011; Luther et al., 2016; Phillips and Katti, 2020), or changes in note rates (Slabbekoorn and den Boer-Visser, 2006; Cartwright et al., 2014), which can affect performance of a physiological tradeoff between repeated and broadband notes (Podos, 1996), and result in lower quality song performance.

A variety of vocal species have performance limits on the rate at which broadband notes can be repeated because of mechanical constraints (e.g., primates: Clink et al., 2018; mice: Pasch et al., 2011; birds: Podos, 1996, 1997). This tradeoff, known as vocal performance, is used in male-male competition (red-winged blackbirds, *Agelaius phoeniceus*: Cramer and Price, 2007; banded wrens, *Thryophilus pleurostictus*: Illes et al., 2006; de Kort et al., 2009; swamp sparrows, *Melospiza georgiana*: Dubois et al., 2011; Moseley et al., 2013; white-crowned sparrows, *Zonotrichia leucophrys*: Phillips and Derryberry, 2017a,b, 2018) and female mate choice (swamp sparrows: Ballentine et al., 2004; Lincoln's sparrows, *Melospiza lincolnii*: Caro et al., 2010; banded wrens: Cramer et al., 2011; canaries, *Serinus canaria*: Drăgănoiu et al., 2002; singing mice (*Scotinomys* spp.): Pasch et al., 2011). Limited research has examined the signaler qualities conveyed by vocal performance to receivers, but in nightingales (*Luscinia megarhynchos*) high performance males are older and sing more consistently (Sprau et al., 2013). In Java sparrows (*Lonchura oryzivora*) performance increases over time, giving listeners reliable information about the age of the singer (Ota and Soma, 2014). Swamp sparrow males with higher performance also are larger and older (Ballentine, 2009), and aggressive intent is also conveyed through vocal performance (DuBois et al., 2009).

One species that persists across urban and rural areas is Nuttall's white-crowned sparrow (*Zonotrichia leucophrys nuttalli*). Nutall's white-crowned sparrows are a year-round resident of the narrow strip of coastal scrub in northern and central California, and have been well-documented in the Bay Area of California for the past 50 years (Baptista, 1975; Petrinovich and Patterson, 1982; Dewolfe et al., 1989). This subspecies sings one song type and is known for forming regional dialects (Baptista, 1975). Once a song is crystallized after the first year, songs are highly repeatable (Phillips and Derryberry, 2017b) and used to attain territories (Dewolfe et al., 1989). Before human settlement, San Francisco consisted of mostly dunes and scrub habitat. This native habitat was largely converted to human use in the late 1800's and early 1900's, with remaining natural areas often converted from scrub to forests of blue gum eucalyptus (*Eucalyptus globulus*), Monterey pine (*Pinus radiata*), and Monterey cypress (*Cupressus macrocarpa*) (McClintock, 2001). A long-term study in Point Reyes, California, showed that as Douglas fir (*Pseudotsuga menziesii*) forest regenerated between 1981 and 2001, densities of breeding *Z. l. nuttalli* decreased, supporting that this sub-species prefers open scrub habitat rather than dense forests for breeding and foraging (Chase et al., 2005). Despite these changes in habitat, *Z. l. nuttalli* persists in urban San Francisco, with higher apparent survival, though lower body condition, than rural birds (Phillips et al., 2018b). Further, minimum frequency and vocal performance vary with urban and rural soundscapes (Derryberry et al., 2016; Luther et al., 2016).

While anthropogenic noise and habitats select for higher pitched, narrow bandwidth songs that transmit better in noise (Slabbekoorn et al., 2007; Grabarczyk and Gill, 2019; Phillips et al., 2020), urban white-crowned sparrows still seem to use vocal performance to assess competitors in urban habitats (Phillips and Derryberry, 2018). Thus, given that performance functions in male-male competition even in noisy urban areas, the question remains whether vocal performance signals a male's quality and ability to obtain higher quality territories under varying levels of noise and urban habitats. Here, we test three hypotheses within the urban-rural matrix in the Bay Area of California using the Nuttall's white-crowned sparrow (*Z. l. nuttalli*). First, to explore the hypothesis that vocal performance is indicative of male quality, we examine whether physical characteristics associated with male condition are related to vocal performance, namely scaled mass index and fat score. We predict that higher performers are in better body condition and have more fat reserves compared to lower performers. Next, to assess whether noise affects vocal performance across the urban-rural matrix, we examine whether vocal performance varies with noise at three levels: dialect region, location, and territory. We expect that vocal performance decreases as noise levels increase across all dialect regions, locations, and at the territory level (Luther et al., 2016). We additionally examine noise, ecological characteristics and vocal performance between urban and rural locations, and expect that urban areas are noisier and urban birds have lower performance. Lastly, we test if territory quality varies with vocal performance scores using remotely sensed ecological variables to assess habitat quality. We expect that high performers will hold higher quality territories, with less human influenced characteristics like introduced trees, more native scrub for nesting, flat and open ground for foraging, higher greenness, and less drought stress.

METHODS

Avian Sampling and Condition Measurements

In 2016, we identified 93 male white-crowned sparrow territories across urban San Francisco region ($N = 60$) and rural Point Reyes ($N = 33$). Six regions were sampled, where each region has a different song dialect. In urbanized areas, the Presidio region sings the San Francisco dialect ($N = 28$), the Fort Funston region sings a San Francisco and San Francisco-Lake Merced hybrid dialect ($N = 19$) (Luther and Baptista, 2010), and the Richmond region sings the Berkeley dialect ($N = 13$) (Baptista, 1975). In Point Reyes, the Limantour region sings the Limantour dialect ($N = 14$), the Abbott's Lagoon region sings both McClure and Drake dialects ($N = 12$), and the Commonweal sings the Clear dialect ($N = 7$) (Baker and Thompson, 1985). Ten locations were sampled and assessed as an individual category to account for spatial correlation, where San Francisco had five locations (Battery East, Battery West, Fort Scott, Lobos Dunes, and Baker Beach) and all other regions only had one location (Fort Funston, Richmond, Commonweal, Abbott's Lagoon, and Limantour). Males were caught with mist-nets and color-banded for individual identification then released at the same locations where they were caught. During capture, JNP measured tarsus using a SPI Polymid Dial Caliper and measured body mass using a Pesola Micro Spring Scale. Fat was scored based on the furcular hollow on a 0–5 scale, where 0 = no fat, 1 = trace amounts, 2 = 1/3 full, 3 = 2/3 full, 4 = even with breast muscle, and 5 = bursting (Kaiser, 1993; Pyle, 1997). One male was recorded but not captured, thus $N = 92$ for body condition analyses. To account for structural body size, we calculated a scaled mass index following Peig and Green (2009). Briefly, we calculated the standardized major axis (SMA) regression slope of mass vs. tarsus length from a larger historic sample ($N = 239$) of Nuttall's white crowned sparrows, and used the average tarsus length from the full population (Phillips et al., 2018b). Examination of SMA residual vs. fitted values and QQ plots indicated a linear relationship between tarsus and mass. All work was approved by Tulane University Institutional Animal Care and Use Committee (protocol 0427-R), USGS Bird banding Laboratory Permit (23900), California State Collecting Permit (6799), Golden Gate National Recreation Area Scientific Research and Collecting Permit (GOGA-00079), San Francisco Parks and Recreation Permit (032014), and Point Reyes National Park Scientific Research and Collecting Permit (PORE-0014).

Recording and Song Analyses

Each male was recorded either immediately prior to capture or on a subsequent day as identified by individual color

TABLE 1 | Remote sensing variables.

Metric	Source	Units	Description	References
NDVImean	Landsat 8 OLI		Average NDVI value across area	Huete et al., 2002
NDWImean	Landsat 8 OLI		Average NDWI value across area	Huete et al., 2002
MeanCHM	LiDAR	m	Mean height in meters of canopy vegetation	
LAD1	LiDAR	m^2/m^3	One-sided leaf area within a given vertical strata. Describes vertical and horizontal structure variances within vegetation across different height intervals. Leaf area density calculated from 0 to 3 m above the ground. This function computes a leaf area density profile	Bouvier et al., 2015
LAD2	LiDAR	m^2/m^3	Leaf area density calculated for vegetation above 3 m above the ground. This function computes a leaf area density profile based on the method of Bouvier et al.	Bouvier et al., 2015
zmax	LiDAR	m	Maximum height	
pground	LiDAR	%	Percentage of returns classified as "ground"	
mSlope	LiDAR	Degrees	Mean slope across measurement area	

bands. To record songs, we used a Sony PBR 400 parabolic reflector with a Sennheiser ME62 omnidirectional microphone (Wedemark, Germany), foam windscreen, and Marantz PMD 661 recorder (Kanagawa, Japan). We analyzed approximately 1–10 songs per male (mean ± SD: 4.85 ± 3.90). One song should be sufficient as white-crowned sparrow songs in these populations are highly repeatable (Phillips and Derryberry, 2017b). Songs were recorded at a sampling rate of 44.1 kHz,.wav files, and resampled to 25 kHz for analysis. Using SIGNAL 5 (Beeman, 1998), songs were high-pass filtered at 1,500 Hz to remove low frequency background noise. We measured trill minimum and maximum frequencies at −36 dB from the peak amplitude frequency (time resolution: 10.2 ms, frequency resolution: 97.7 Hz, 256 pt transform). Bandwidth was calculated as the difference between maximum and minimum frequency, and trill rate was measured as the average number of notes per second (Hz). Wilson et al. (2014) suggested the use of the quantile regression method instead of the upper bound regression method when evaluating whether there was a significant trade-off between trill rate and bandwidth in a population of songs. In that review paper, they assessed the family-wide performance limit for Emberizidae and found that both methods (upper bound and quantile regression) recovered a significant trade-off between trill rate and bandwidth. To make sure our results are comparable to previous studies, we used the measurement of vocal deviation to approximate vocal performance, which was measured as the orthogonal distance from the upper-bound regression of 1,572 Passerellidae songs (formerly Emberizidae), $y = 0.124x + 7.55$ (Podos, 1997). We also conduct all analyses following the recommendations of Wilson et al. (2014) and include the details and results in **Supplement 1**.

TABLE 2A | Model selection table for ten candidate models for Vocal Deviation∼Body Condition.

Candidate models	K	AICc	ΔAICc	w_i	Cumulative w_i	LL
Fat*Type	6	511.43	0.00	0.30	0.30	−249.22
Fat + Scaled Mass Index + Type	6	511.55	0.12	0.28	0.58	−249.28
Scaled Mass Index *Type	6	511.65	0.22	0.27	0.85	−249.33
Fat	4	514.66	3.23	0.06	0.91	−253.10
Scaled Mass Index	4	514.81	3.37	0.06	0.96	−253.17
Fat + Scaled Mass Index	5	516.89	5.46	0.02	0.98	−253.10
Fat* Scaled Mass Index *Type	10	518.28	6.85	0.01	0.99	−247.78
Fat* Scaled Mass Index	6	518.41	6.98	0.01	1.00	−252.71
Type	4	525.91	14.48	0.00	1.00	−258.73
Null	3	531.94	20.51	0.00	1.00	−262.84

TABLE 2B | Conditional model average of the top three models within 2AICc for body condition models.

	Estimate	SE	Z	Lower 95% CI	Upper 95% CI	Importance
(Intercept)	24.91	1.70	14.47	21.54	28.28	
Fat	0.25	0.55	0.45	-0.85	1.35	0.68
Type	6.86	2.06	3.29	2.77	10.95	1
Fat*Type	-0.28	0.81	0.34	-1.88	1.32	0.65
Scaled Mass Index	-0.02	0.48	0.03	-0.97	0.94	0.35
Body Condition*Type	0.18	0.77	0.23	-1.35	1.70	0.32

Noise Level Measures

We measured ambient noise levels male territories between 7:00 AM to 12:00 PM with a class 1 Larson-Davis 831 sound level meter, sampling 5 times per second, fast weighting (PCB Piezetronics). Following Brumm (2004), we recorded A-weighted equivalent continuous noise level (LAeq) for 1 min in each cardinal direction from the center of the territory for a total of 4 min, totaling 12,000 samples that are averaged to a single number for that territory. Units of LAeq (DB re 20 μPa) were used because A-weighting covers approximately the range of sound that birds can hear (Dooling et al., 2000) and accounts for fluctuations of noise during the recording. All noise recordings were taken in the absence of wind (3 > Beaufort Wind scale) and actively singing birds.

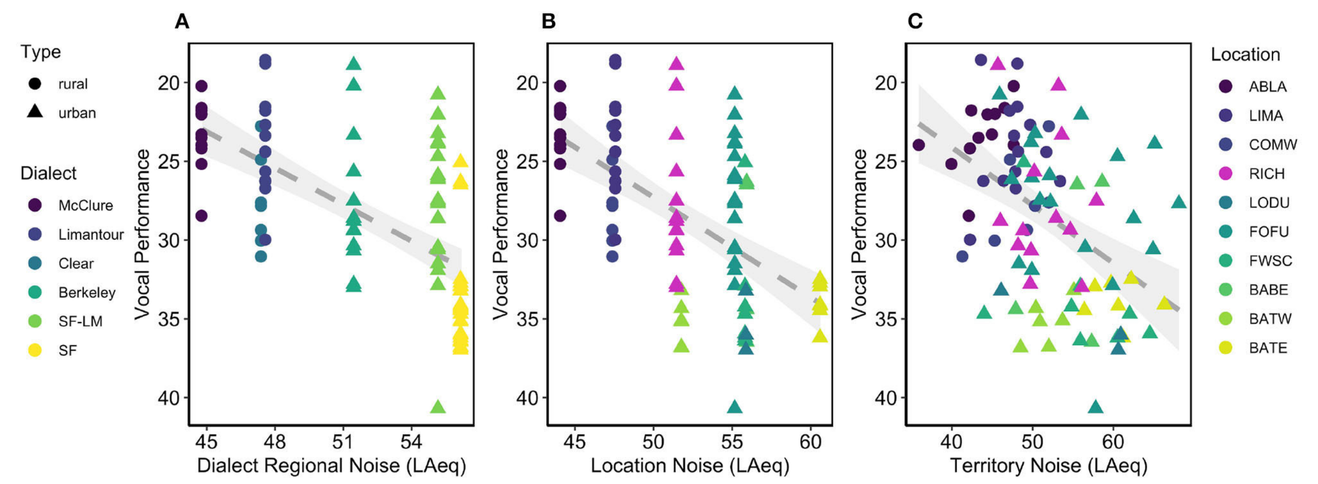

FIGURE 1 | (A) Urban regions have higher noise and lower performance songs. **(B)** Urban locations are also noisier and have lower performance songs. **(C)** High performers have quieter territories. Line of best fit and 95% standard error for each model shown in gray.

Territory Quality Measures

Remote sensors have proven beneficial in performing repeated standardized measurements over large areas testing for relationships between habitat selection and ecological gradients with high resolution and accuracy (Roughgarden et al., 1991; Smith et al., 2013). Sensors such as Landsat from satellites have been used for decades to estimate environmental variables on the ground and relate to species diversity (Pettorelli et al., 2014; Rocchini et al., 2016). Other sensors such as Light Detection and Ranging (LiDAR) have greatly improved the resolution of these data compared to satellites and are able to capture environmental information at resolutions less than one square meter (Farrell et al., 2013; Davies and Asner, 2014; He et al., 2015). These measures have also been used to designate habitats related to the occurrence of individual species (Clawges et al., 2008) and to understand how habitat heterogeneity relates to richness as a whole (Goetz et al., 2007). The information from these sensors provides great potential to investigate relationships between animals, plants, and environmental variables at both fine and large scales across landscapes.

We used two LiDAR datasets from projects around the San Francisco Bay Area to get accurate vegetation measures across all study sites. One dataset was from the Golden Gate LiDAR Project (GGLP), which was collected for the United States Geological Survey (USGS) in 2010 (OCM Partners, 2010). The second LiDAR dataset was collected by NOAA's Office for Coastal Management in the northern San Francisco Bay area in 2010 (Office for Coastal Management, 2010). LiDAR height returns were normalized to eliminate any elevational difference in points before calculating standard ground metrics using the "lidR" package in R version 3.3.2 (Roussel and David, 2018). In addition to LiDAR, we used imagery collected by Landsat 8 Operational Land Imager (OLI) during August of 2015 to calculate productivity indices. The datasets and specific images were selected to be as close as possible to the time of white-crowned sparrow observations while covering all sites.

TABLE 3A | Nine Candidate models for the effects of noise (Dialect Regional Noise, Location Noise, and Territory Noise) and habitat type on vocal deviation.

Candidate models	K	AICc	ΔAICc	w_i	Cumulative w_i	LL
Dialect LAeq	3	530.25	0.00	0.48	0.48	−261.99
Dialect Laeq + Type	4	530.89	0.64	0.35	0.82	−261.22
Dialect LAeq*Type	5	532.29	2.04	0.17	0.99	−260.80
Location LAeq	3	540.27	10.02	0.00	1.00	−267.00
Location LAeq + Type	4	541.15	10.90	0.00	1.00	−266.35
Location LAeq*Type	5	543.36	13.11	0.00	1.00	−266.34
Territory LAeq + Type	4	543.62	13.37	0.00	1.00	−267.58
Territory LAeq*Type	5	544.53	14.28	0.00	1.00	−266.92
Type	3	545.06	14.81	0.00	1.00	−269.39
Territory LAeq	3	555.54	25.29	0.00	1.00	−274.64
Null	2	576.02	45.77	0.00	1.00	−285.94

TABLE 3B | Conditional model average of the top three models within 2AICc.

	Estimate	SE	Z	Lower 95% CI	Upper 95% CI	Importance
(Intercept)	-17.11	10.80	1.57	-38.47	4.24	
Dialect LAeq	0.89	0.23	3.84	0.44	1.35	1
Type	-2.82	2.29	1.21	-7.38	1.74	0.42

A set of nine metrics was selected to determine habitat quality over a 50 m radius from the center of each White-crowned Sparrow territory, as the average territory size in white-crowned sparrows is approximately 1 hectare (Morton, 1992). The leaf area density (LAD) was selected to accurately measure productivity within 50 m of each activity center for two vertical strata above the ground: undergrowth (LAD1: 0.5–2 m) and canopy vegetation (LAD2: >2 m) (Kamoske et al., 2019).

TABLE 4 | Mean and SD for ecological variables for urban and rural samples with results from Welch's *t*-tests for each variable.

Variables	URBAN	RURAL	T	DF
LAeq	54.71 ±5.92	46.25 ±3.76	8.55	93.65
LAD1	0.16 ±0.15	0.08 ±0.08	−3.21	90.83
LAD2	0.03 ±0.03	0.006 ±0.01	−4.97	87.27
MeanCHM	2.44 ±3.04	0.52 ±1.66	−3.87	90.86
pground	53.56 ±29.63	65.15 ±14.75	2.48	90.79
mSlope	0.17 ±0.10	0.13 ±0.07	−2.35	89.22
zmax	16.12 ±12.30	5.39 ±6.50	−5.45	91.00
NDVImean	0.19 ±0.06	0.23 ±0.05	3.50	77.08
NDWImean	0.04 ±0.05	−0.02 ±0.05	−5.64	66.04

TABLE 5 | Candidate Models for Vocal Deviation ∼ Habitat Quality.

Candidate models	K	AICc	ΔAICc	w_i	Cumulative w_i	LL
LAD2 + mSlope + Type	6	521.12	0.00	0.13	0.13	−254.07
LAD1 + MeanCHM + zmax + Type	7	521.36	0.24	0.12	0.25	−253.02
LAD2 + mSlope + zmax + Type	7	521.59	0.47	0.10	0.35	−253.14
LAD2 + mSlope + zmax + MeanCHM + Type	8	521.63	0.51	0.10	0.45	−251.96
LAD1 + MeanCHM + NDVI + zmax + Type	8	522.03	0.91	0.08	0.54	−252.16
LAD2 + mSlope + NDVI + Type	7	522.25	1.13	0.07	0.61	−253.47
LAD2 + mSlope + pground + Type	7	522.34	1.22	0.07	0.68	−253.51
LAD1 + MeanCHM + LAeq + zmax + Type	8	522.72	1.60	0.06	0.74	−252.50
LAD2 + MeanCHM + mSlope + NDVI + zmax + Type	9	522.86	1.74	0.06	0.80	−251.35
LAD2 + mSlope + NDVI + zmax + Type	8	522.97	1.85	0.05	0.85	−252.63
LAD1 + LAD2 + MeanCHM + zmax + Type	8	523.00	1.88	0.05	0.90	−252.64
LAD1 + LAeq + MeanCHM + NDVI + zmax + Type	9	523.09	1.97	0.05	0.95	−251.46
MeanCHM + mSlope + zmax + Type	7	523.12	2.00	0.05	1.00	−253.90
Null	3	531.94	10.82	0.00	1.00	−262.84

Other standard LiDAR and Landsat metrics were calculated for each area as listed in **Table 1**. The Normalized Difference Water Index (NDWI) was derived from the Landsat 8 OLI imagery, and was used as a surrogate for drought stress, where a high value indicates high water content within vegetation and soil (Gao, 1996). We calculated the mean NDWI values for each territory using the "raster" package in R version 3.3.2 (Robert, 2020). In addition to these habitat measurements, the average slope, aspect, and elevation were derived from the raw LiDAR dataset.

To reduce collinearity of the ecological fixed effects, we examined spatial autocorrelation of 64 ecological variables extracted from remote sensing measures. Because of high correlation of many variables, we first reduced our independent factors to NDVI mean, NDWI mean, percent bare ground cover (pground), mean height of canopy vegetation (MeanCHM), mean slope, mean aspect, elevation, understory leaf area density 0–3 meters (LAD1), canopy leaf area density 3 meters and above (LAD2), overall territory height (Zmax). We further examined collinearity with variance inflation factors (VIF), which showed that all variables had a VIF < 6, so all nine variables were retained in the global model.

Statistical Analyses

All analyses were conducted in R (R Core Team, 2020) using lme4 and AICmodavg to explore candidate models with AICc (Bates et al., 2015; Mazerolle, 2020). First, we examined whether body condition characteristics of individuals correlated to vocal deviation. We used a conservative approach and used our scaled mass index to estimate body condition. We then examined linear mixed models with fixed effects of Fat Score, Scaled Mass Index, and Type (urban/rural), with location as a random effect to account for any spatial autocorrelation (total nine candidate models). Next, we explore linear models to examine whether vocal deviation varied with noise levels (LAeq) at three levels—across dialects (Dialect Noise), across locations (Location Noise), and within territories (Territory Noise). We also explore candidate models for the additive and interactive effect of Type (urban/rural), which totaled eleven candidate models. Additionally, we used *t*-tests to compare average noise levels and territory characteristics between urban and rural birds. Lastly, to understand how territory quality correlates to vocal performance, we examined linear mixed effect models with deviation as the dependent variable, location as the random effect to take into account spatial variation, and ecological variables measured on territories, including Territory Noise level (LAeq) and Type (urban/rural), as fixed effects. We used the dredge function in MuMIn to explore all possible additive models, and examined candidate models within 2AICc (Arnold, 2010). For all model selection analyses, we used MuMIN to examine the model average of models within 2AICc when necessary (Bartoń, 2020) and report 95% CI intervals. If Type was a significant factor in the model average, we also conducted model selection and model averaging in the urban subset alone and the rural subset alone to clarify directionality of effects. If the random factor Location was equivalent to zero, we instead examined linear models (Bates et al., 2018).

RESULTS

Habitat Type Predicts Deviation Over Body Condition

We examined ten candidate models with Location as a random effect, where the top three models were within 2 AICc of each other (**Table 2A**). The highest ranked model included fat score interacting with Type and Location as a random effect (ER = 2,985, $w_i = 0.29$, Location variance = 7.52, SD = 2.74, **Table 2A**), followed by a model with Fat + Scaled Mass Index + Type

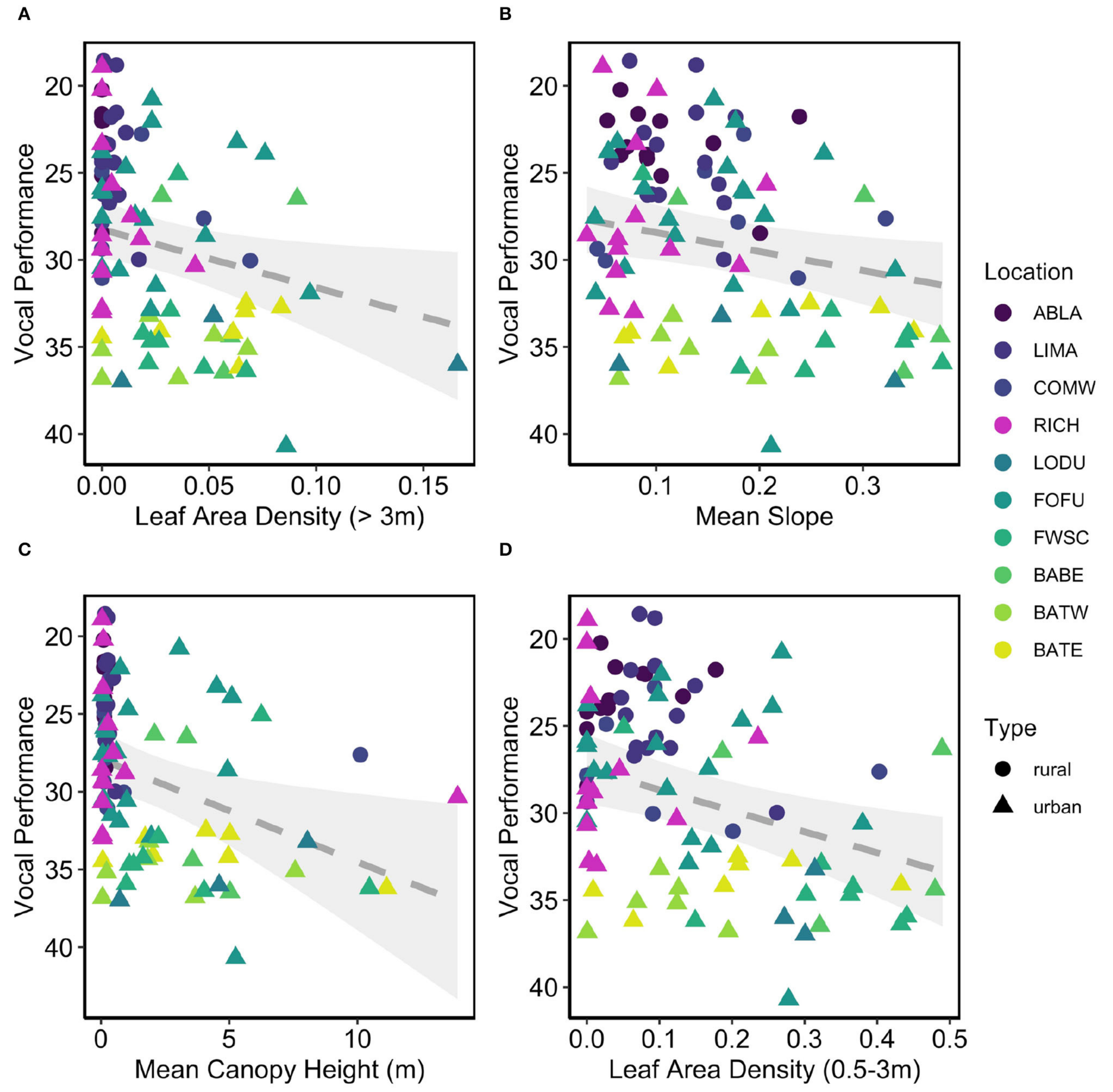

FIGURE 2 | Low performance males (high deviation) have territories with **(A)** denser canopies, **(B)** steeper slopes, **(C)** higher canopies, and **(D)** denser understories. Gray dotted line and band denotes line of best fit with standard error (A&B candidate model 1, C&D candidate model 6).

(ER = 2,800, $\boldsymbol{w_i}$ = 0.28, Location variance = 15.54, SD = 3.94, **Table 2A**), and Scaled Mass Index*Type (ER = 2,700, $\boldsymbol{w_i}$ = 0.27, Location Variance = 7.48, SD = 2.74). The conditional model average supported strong effects of Type on vocal performance, rather than Fat or Scaled Mass Index (**Table 2B**). Our analyses with quantile regression performance values also supported the effect of Type over body condition measures (**Supplement 1**, **Table S1**). Rural birds had higher performance than urban birds (deviation mean ± SD. Urban: 30.54 ± 4.99, Rural: 24.56 ± 3.16).

Performance Is Related to Noise Level

Noise had a negative effect on performance, and was significant at three levels (Dialect Region, Location, and Territory; **Figure 1**). However, only two candidate models were within 2 AICc, where Dialect Region noise had the most important influence on vocal deviation ($\beta = 0.77$, SE = 0.10, $F_{1,\,91} = 61.32$, 95% CI = 0.58–0.97, **Table 3A**, **Figure 1A**), followed by Dialect Region noise + Type (Dialect Region noise: $\beta = 1.06$ SE = 0.25, 95% CI = 0.55–1.57; Type: $\beta = -2.82$, SE = 2.29, 95% CI = −7.38–1.74; $F_{2,90}$ = 31.58, **Table 3A**, model average **Table 3B**). Males in quieter

TABLE 6 | Model Averaged Coefficients for Vocal Deviation~Ecological Variables.

	Estimate	SE	Z	Lower 95% CI	Upper 95% CI	Importance
(Intercept)	25.24	1.40	17.75	22.45	28.03	
LAD2	1.10	0.55	1.97	0.00	2.19	0.64
mSlope	1.17	0.47	2.44	0.23	2.11	0.64
Type	5.88	1.79	3.25	2.33	9.43	1.00
LAD1	1.55	0.53	2.87	0.49	2.62	0.36
MeanCHM	1.63	0.79	2.04	0.06	3.19	0.57
zmax	−1.68	0.95	1.75	−3.57	0.20	0.72
NDVImean	0.51	0.43	1.18	−0.34	1.36	0.31
pground	0.75	0.70	1.05	−0.65	2.14	0.07
LAeq	0.55	0.51	1.08	−0.45	1.56	0.11

locations have higher performance ($\beta = 0.74$, SE = 0.09, $F_{1,\,91} = 60.97$, 95% CI = 0.55–0.93, **Figure 1B**). Across territories, males that produce higher performance songs defend territories with lower noise levels ($\beta = 0.37$, SE = 0.07, $F_{1,\,91} = 25.05$, 95% CI = 0.22–0.51, **Figure 1C**). As above, rural birds produced songs with higher vocal performance than did urban birds ($\beta = 6.00$, SE = 0.96, $t = 6.24$, $F_{1,\,91} = 38.9$, 95% CI = 4.08–7.89). Model selection and model averaging from quantile regression also supported effects of Dialect Region noise, Location noise, and Territory noise on vocal performance (**Supplement 1**).

Characterization of Urban and Rural Territories

Urban territories had higher noise levels than rural territories (**Table 4**). Overall, urban territories had higher leaf area densities in the understory (LAD1) and canopy (LAD2). Canopies of urban territories were taller at maximum height (zmax) and on average (MeanCHM). Rural areas had more open ground (pground) with less sloped terrain (mSlope), more greenness (NDVImean) and more drought stress (NDWImean) (**Table 2**).

High Performers Are on Flatter Territories With Less Leaf Area Density and Lower Canopies

We examined 13 candidate models that were within 2AIC, all of which include Type as a fixed effect, and a null model for a total of 14 models. The highest ranked model included leaf area density for canopy above 3 m (LAD2) and mean slope (mSlope), where both variables had a positive correlation with vocal deviation, meaning lower performers had territories with higher canopy leaf density and steeper slopes (ER = 1,300, Location variance = 3.86, SD = 2.00, **Table 5**, **Figures 2A,B**). The next ranked model included leaf area density below 3 m (LAD1, **Figure 2C**), mean canopy height (MeanCHM, **Figure 2D**), and maximum height (zmax) (ER = 1,200, Location variance = 4.93, SD = 2.22, **Table 5**). Model averaged estimates and importance values supported the top model (**Table 6**, **Figure 3**), as well as showed significant effects of leaf area density below 3 meters (LAD1) and mean canopy height (**Figure 3**). Low performers were on territories with steeper slopes, denser and higher average canopy and denser understories (**Figures 2**, **3**). Models estimating performance from quantile regression show similar patterns, where low performers were significantly on territories with steeper slopes and less dense canopies and understories (**Supplement 2**).

Because Type had the strongest effect on deviation, we also ran model selection within habitat types. Within urban habitats, 10 models were within 2AICc (**Supplement 2A**). Higher performers were on territories with shorter average canopies but taller maximum heights, which includes man-made structures (**Supplement 2B**, **Figure 3**). Additionally, urban high performers had less dense understories (**Supplement 2B**, **Figure 3**). Within rural habitats, higher performers were on territories with significantly less dense canopies (**Supplement 3**, **Figure 3**). Analyses for performance with quantile regression show similar patterns, with urban high performers on territories with less dense understories and lower canopy heights (**Supplement 1**). Rural birds tended to have less dense canopies (**Supplement 1**).

DISCUSSION

Vocal performance of male white-crowned sparrows correlates with background noise levels and landscape features of the breeding territories they defend, but not with body condition. Consistent with our predictions, we found that high performance males hold flatter territories with lower noise levels and short native scrub habitat. Conversely, low performance males hold territories with higher noise levels and dense, taller vegetation, which is a product of human settlement in the coastal regions of the Bay Area (McClintock, 2001). Together, our results suggest that vocal performance may signal the ability to obtain and defend territories that are in favored habitat (i.e., low laying scrub and grassland), which should improve their chance of survival and successful breeding. To our knowledge, only one study shows a similar link between song characteristics and habitat quality (Manica et al., 2014). Since high performance males are on quieter territories, with less dense understories and less canopy cover, selection pressure on song transmission should also be released, reducing constraints on vocal performance. These findings link together fundamental aspects of sexual selection in that habitat quality and the quality of sexually selected signals appear to be associated: males with the highest performing songs are defending territories of the highest quality.

We hypothesized that that high performers may be more competitive at holding territories with better food sources, and therefore be in better body condition. However, we did not find evidence for fat score or scaled mass index correlating with vocal performance. This could be due to sample size, lack of heterogeneity in food availability across our sites, or possibly there are other metrics of body condition that are important that we did not consider in our methods. The sampling year (2016) was a wet year compared to the previous 4 years, which may have erased any large disparities in food or water availability between urban and rural locations. Cities typically present a greater patchwork of available resources, such as bird feeders,

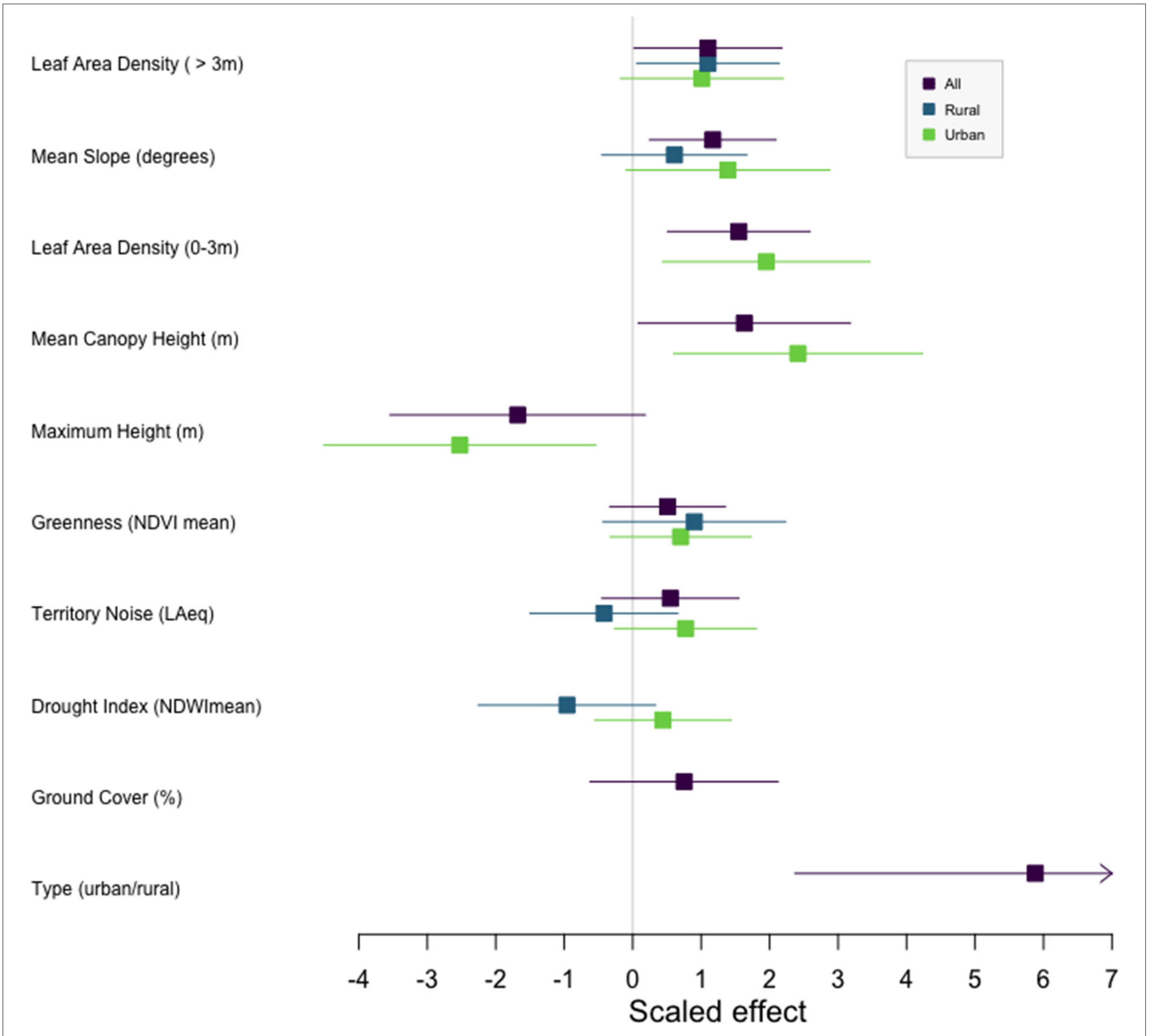

FIGURE 3 | Effects plot for the model average of 13 candidate models across urban and rural locations (All), 10 candidate models within urban areas (Urban), and 7 candidate models within rural areas (Rural). Variables to the left of zero have a negative effect on vocal deviation, and are associated with higher performance songs, while variables to the right have a positive effect on vocal deviation, indicating an association with lower performance songs. Boxes denote mean and lines denote 95% confidence intervals.

green space, and large tracts of cement (Robb et al., 2008), which may create "boom or bust" dynamics, but a wet winter may nullify these dynamics across both urban and rural areas. The 2015-2016 wet season produced 23.21 inches of rain in San Francisco, which is within the average range from 1849 to 2019 (21.86 ± 7.5 inches per season, https://www.ggweather.com/sf/monthly.html). Therefore, our sampling year would have had high productivity for birds, likely due to increased plant and insect food resources related to rainfall (Desante and Geupel, 1987; Dybala et al., 2013), potentially resulting in similar body condition across habitats. Previous studies found body size to vary with urbanization level (Meillère et al., 2015), but whether song performance is related to body condition across urban ecosystems remains to be seen. Future research within long-term research areas will allow for larger sample sizes and the ability to account for yearly variation and would greatly benefit our understanding of the relationship between song and male quality.

Anthropogenic noise interferes with communication (Slabbekoorn, 2013), foraging vigilance (Ware et al., 2015), and reproductive fitness in many species (Injaian et al., 2018; Kleist et al., 2018; Gurule-Small and Tinghitella, 2019). Therefore, there may be a fitness benefit to avoiding noise, such that individuals are likely to be more successful in attracting mates, feeding chicks, and fledging offspring when on territories with lower noise levels. Our study system has consistently shown that urban San Francisco has higher noise levels, particularly at low frequencies as compared to nearby rural Point Reyes (Lee and MacDonald, 2011, 2013; Derryberry et al., 2016; Phillips and Derryberry, 2017b; Phillips et al., 2018b), and that song varies with ambient and background noise levels (Derryberry et al., 2016), including vocal performance characteristics (Luther et al., 2016). Our additional data are in line with previous findings that noise levels are related to vocal performance. Territory noise levels were predictive of vocal performance across dialects, consistent with our previous work within the San Francisco dialect (Luther et al., 2016).

High performers hold flatter territories with more scrub and less trees. These characteristics are beneficial to the scrub adapted Nuttall's white-crowned sparrow (Chase et al., 2005). Flatter ground provides foraging habitat and open space to observe predators, while low shrubs like coyote brush (*Baccharus pilularis*), lupine spp. (*Lupinus spp.*), California blackberry (*Rubus ursinus*), and poison oak (*Toxicodendron diversilobum*) provide nesting habitat and places to hide from predators. Additionally, many of the areas in San Francisco that retain native scrub are on cliffsides where human development is not possible, so competition for flatter territories is likely high. In this study and in previous work (Phillips et al., 2018a), we have observed that urban parks within the Bay Area are landscaped with taller, non-native shrubs and trees. Our remotely sensed leaf area density measures and mean canopy height measure suggest that low performers are on territories with taller trees and thicker vegetation, which is not preferred habitat for white-crowned sparrows (Chase et al., 2005). This trend is especially notable within the urban habitat. Previously in this system, percent tree cover as measured from Google Earth imagery indicated that more trees are found on urban territories (Phillips et al., 2018a). Together, it seems likely that high performance males are more competitive and thus better able to acquire territories with species-preferred characteristics, such as low laying native scrub with adjacent open space.

High performance males may be on territories with species-preferred scrub habitat because they are more competitive or because their signal transmits better on these more open territories, or both. Taller, denser vegetation results in more reverberation and degradation of trilled signals which over time selects for reduced trill rates and narrow bandwidth (Morton, 1975; Derryberry, 2009; Phillips et al., 2020), whereas trilled vocalizations are less constrained on more open habitats and can evolve to faster rates and wider bandwidth (Wiley, 1991), at least until a physical performance constraint is met (Podos, 1997). Therefore, males with high performance songs may select territories based on transmission properties, or just be more successful during conflict with low performance competitors because their song transmits better and/or indicates higher competitive abilities. Multiple recaptures and recordings of males throughout the breeding season, starting at territory establishment, can inform whether high performance males are more competitive and this is the driver of territory holding ability, or if song transmission alone ultimately leads to higher success at obtaining and defending territories with lower noise levels in species-preferred habitat.

Conclusions

Our results are the first to show a relationship between vocal performance, a physically limited song trait, and territory quality. This study provides a first step toward understanding how urban landscapes and soundscapes affect song evolution and thus reproduction and survival. Future research linking reproductive outcomes across a variety of performers and landscapes will provide important insights into how anthropogenic pollution may affect not only animal behavior but also fitness and the longer-term stability of populations.

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 Tulane University Institutional Animal Care and Use Committee (protocol 0427-R), USGS Bird banding Laboratory Permit (23900), California State Collecting Permit (6799), Golden Gate National Recreation Area Scientific Research and Collecting Permit (GOGA-00079), San Francisco Parks and Recreation Permit (032014), and Point Reyes National Park Scientific Research and Collecting Permit (PORE-0014).

AUTHOR CONTRIBUTIONS

JP, ED, and DL conceived and designed the study. JP collected field data and WC extracted LiDAR and Landsat variables. JP ran the statistics, wrote the manuscript with input, and final approval from WC, ED, and DL. 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.2020.587120/full#supplementary-material

REFERENCES

Andersson, M. B. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press. doi: 10.1515/9780691207278

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *J. Wildl. Manage.* 74, 1175–1178. doi: 10.1111/j.1937-2817.2010.tb01236.x

Aronson, M. F. J., Nilon, C. H., Lepczyk, C. A., Parker, T. S., Warren, P. S., Cilliers, S. S., et al. (2016). Hierarchical filters determine community assembly of urban species pools. *Ecology* 97, 2952–2963. doi: 10.1002/ecy.1535

Aronson, M. F. J., Sorte, F. A., La Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., et al. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc. R. Soc. B* 281:20133330. doi: 10.1098/rspb.2013.3330

Baker, M. C., and Thompson, D. B. (1985). Song dialects of white-crowned sparrows: historical processes inferred from patterns of geographic variation. *Condor* 87, 127–141. doi: 10.2307/1367144

Ballentine, B. (2009). The ability to perform physically challenging songs predicts age and size in male swamp sparrows, Melospiza georgiana. *Anim. Behav.* 77, 973–978. doi: 10.1016/j.anbehav.2008.12.027

Ballentine, B., Hyman, J., and Nowicki, S. (2004). Vocal performance influences female response to male bird song: an experimental test. *Behav. Ecol.* 15, 163–168. doi: 10.1093/beheco/arg090

Baptista, L. F. (1975). Song dialects and demes in sedentary populations of the white-crowned sparrow (Zonotrichia leucophrys nuttalli). *Univ. Calif. Publ. Zool.* 105, 1–52.

Bartoń, K., (2020). *MuMIn: Multi-Model Inference*. R package version 1.43.17. Available online at: https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. doi: 10.18637/jss.v067.i01

Bates, D., Kliegl, R., Vasishth, S., and Baayen, H. (2018). *Parsimonious Mixed Models. arXiv* 1506.04967. Available online at: http://arxiv.org/abs/1506.04967 (accessed November 30, 2020).

Beeman, K. (1998). "Digital signal analysis, editing, and synthesis," in *Animal Acoustic Communication: Sound Analysis and Research Methods*, eds S. L. Hopp, M. J. Owren, and C. S. Evans (Berlin: Springer-Verlag).

Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. *Ecol. Soc.* 6, 506–519. doi: 10.2307/2269387

Bouvier, M., Durrieu, S., Fournier, R., a, and Renaud, J., (2015). Generalizing predictive models of forest inventory attributes using an area-based approach with airborne las data. *Remote Sens. Environ.* 156, 322–334. doi: 10.1016/j.rse.2014.10.004

Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* 73, 434–440. doi: 10.1111/j.0021-8790.2004.00814.x

Caro, S. P., Sewall, K. B., Salvante, K. G., and Sockman, K. W. (2010). Female Lincoln's sparrows modulate their behavior in response to variation in male song quality. *Behav. Ecol.* 21, 562–569. doi: 10.1093/beheco/arq022

Cartwright, L. A., Taylor, D. R., Wilson, D. R., and Chow-Fraser, P. (2014). Urban noise affects song structure and daily patterns of song production in Red-winged Blackbirds (*Agelaius phoeniceus*). *Urban Ecosyst.* 17, 561–572. doi: 10.1007/s11252-013-0318-z

Catchpole, C. K., and Slater, P. J. B. (2008). *Bird Song: Biological Themes and Variations. 2nd Edn.* New York, NY: Cambridge University Press. doi: 10.1017/CBO9780511754791

Chase, M. K., Holmes, A. L., Gardali, T., Ballard, G., Geupel, G. R., and Nur, N. (2005). Two decades of change in a coastal scrub community : songbird responses to plant succession 1. *USDA For. Serv. Gen. Tech. Rep.* 613–616. Available online at: https://www.fs.fed.us/psw/publications/documents/psw_gtr191/psw_gtr191_0613-0616_chase.pdf

Clarkson, C. E. (2007). Food supplementation, territory establishment, and song in the prothonotary warbler. *Wilson J. Ornithol.* 119, 342–349. doi: 10.1676/04-073.1

Clawges, R., Vierling, K., Vierling, L., and Rowell, E. (2008). The use of airborne lidar to assess avian species diversity, density, and occurrence in a pine/aspen forest. *Remote Sens. Environ.* 112, 2064–2073. doi: 10.1016/j.rse.2007.08.023

Clink, D. J., Charif, R. A., Crofoot, M. C., and Marshall, A. J. (2018). Evidence for vocal performance constraints in a female nonhuman primate. *Anim. Behav.* 141, 85–94. doi: 10.1016/j.anbehav.2018.05.002

Cramer, E. R. A., Hall, M. L., de Kort, S. R., Lovette, I. J., and Vehrencamp, S. L. (2011). Infrequent extra-pair paternity in the banded wren, a synchronously breeding tropical passerine. *Condor* 113, 637–645. doi: 10.1525/cond.2011.100233

Cramer, E. R. A., and Price, J. J. (2007). Red-winged blackbirds Ageliaus phoeniceus respond differently to song types with different performance levels. *J. Avian Biol.* 38, 122–127. doi: 10.1111/j.2006.0908-8857.03839.x

Croci, S., Butet, A., and Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits? *Condor* 110, 223–240. doi: 10.1525/cond.2008.8409

Davies, A. B., and Asner, G. P. (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends Ecol. Evol.* 29, 681–691. doi: 10.1016/j.tree.2014.10.005

de Kort, S. R., Eldermire, E. R. B., Cramer, E. R., a, and Vehrencamp, S. L. (2009). The deterrent effect of bird song in territory defense. *Behav. Ecol.* 20, 200–206. doi: 10.1093/beheco/arn135

Derryberry, E. P. (2009). Ecology shapes birdsong evolution: variation in morphology and habitat explains variation in white-crowned sparrow song. *Am. Nat.* 174, 24–33. doi: 10.1086/599298

Derryberry, E. P., Danner, R. M., Danner, J. E., Derryberry, G. E., Phillips, J. N., Lipshutz, S. E., et al. (2016). Patterns of song across natural and anthropogenic soundscapes suggest that white-crowned sparrows minimize acoustic masking and maximize signal content. *PLoS ONE* 11, e0154456. doi: 10.1371/journal.pone.0154456

Desante, D. F., and Geupel, G. R. (1987). Landbird productivity in central coastal California: the relationship to annual rainfall, and a reproductive failure in 1986. *Condor* 89, 636–653. doi: 10.2307/1368653

Desrochers, A. (1989). Sex, dominance, and microhabitat use in wintering black-capped chickadees: a field experiment. *Ecology* 70, 636–645. doi: 10.2307/1940215

Dewolfe, B. B., Baptista, L., and Petrinovich, L. (1989). Song development and territory establishment in Nuttall's white-crowned sparrows. *Condor* 91, 397–407. doi: 10.2307/1368318

Dooling, R. J., Lohr, B., and Dent, M. L. (2000). "Hearing in birds and reptiles," in *Comparative Hearing: Birds and Reptiles*, eds R. J. Dooling, A. N. Popper, and R. R. Fay (New York, NY: Springer-Verlag), 308–359. doi: 10.1007/978-1-4612-1182-2_7

Dowling, J. L., Luther, D. A., and Marra, P. P. (2011). Comparative effects of urban development and anthropogenic noise on bird songs. *Behav. Ecol.* 23, 201–209. doi: 10.1093/beheco/arr176

Drăgănoiu, T. I., Nagle, L., and Kreutzer, M. (2002). Directional female preference for an exaggerated male trait in canary (Serinus canaria) song. *Proc. R. Soc. B* 269, 2525–2531. doi: 10.1098/rspb.2002.2192

DuBois, A. L., Nowicki, S., and Searcy, W. A. (2009). Swamp sparrows modulate vocal performance in an aggressive context. *Biol. Lett.* 5, 163–165. doi: 10.1098/rsbl.2008.0626

Dubois, A. L., Nowicki, S., and Searcy, W. A. (2011). Discrimination of vocal performance by male swamp sparrows. *Behav. Ecol. Sociobiol.* 65, 717–726. doi: 10.1007/s00265-010-1073-2

Dybala, K. E., Eadie, J. M., Gardali, T., Seavy, N. E., and Herzog, M. P. (2013). Projecting demographic responses to climate change: adult and juvenile survival respond differently to direct and indirect effects of weather in a passerine population. *Glob. Chang. Biol.* 19, 2688–2697. doi: 10.1111/gcb.12228

Ekman, J. (1987). Exposure and time use in willow tit flocks: the cost of subordination. *Anim. Behav.* 35, 445–452. doi: 10.1016/S0003-3472(87)80269-5

Farrell, S. L., Collier, B. A., Skow, K. L., Long, A. M., Campomizzi, A. J., Morrison, M. L., et al. (2013). Using LiDAR-derived vegetation metrics for high-resolution, species distribution models for conservation planning. *Ecosphere* 4, 1–18. doi: 10.1890/ES12-000352.1

Gao, B. (1996). NDWI—A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sens. Environ.* 58, 257–266. doi: 10.1016/S0034-4257(96)00067-3

Goetz, S., Steinberg, D., Dubayah, R., and Blair, B. (2007). Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. *Remote Sens. Environ.* 108, 254–263. doi: 10.1016/j.rse.2006.11.016

Grabarczyk, E. E., and Gill, S. A. (2019). Anthropogenic noise masking diminishes house wren (Troglodytes aedon) song transmission in urban natural areas. *Bioacoustics* 29, 518–532. doi: 10.1080/09524622.2019.1621209

Grava, T., Grava, A., and Otter, K. A. (2012). Vocal performance varies with habitat quality in black-capped chickadees (*Poecile atricapillus*). *Behaviour* 149, 35–50. doi: 10.1163/156853912X625854

Grava, T., Grava, A., and Otter, K. A. (2013). Habitat-induced changes in song consistency affect perception of social status in male chickadees. *Behav. Ecol. Sociobiol.* 67, 1699–1707. doi: 10.1007/s00265-013-1580-z

Gurule-Small, G. A., and Tinghitella, R. M. (2019). Life history consequences of developing in anthropogenic noise. *Glob. Chang. Biol.* 25, 1957–1966. doi: 10.1111/gcb.14610

He, K. S., Bradley, B. A., Cord, A. F., Rocchini, D., Tuanmu, M.-N., Schmidtlein, S., et al. (2015). Will remote sensing shape the next generation of species distribution models? *Remote Sens. Ecol. Conserv.* 1, 4–18. doi: 10.1002/rse2.7

Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., and Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens. Environ.* 83, 195–213. doi: 10.1016/S0034-4257(02)00096-2

Illes, A. E., Hall, M. L., and Vehrencamp, S. L. (2006). Vocal performance influences male receiver response in the banded wren. *Proc. R. Soc. B* 273, 1907–1912. doi: 10.1098/rspb.2006.3535

Injaian, A. S., Poon, L. Y., and Patricelli, G. L. (2018). Effects of experimental anthropogenic noise on avian settlement patterns and reproductive success. *Behav. Ecol.* 29, 1181–1189. doi: 10.1093/beheco/ary097

Kaiser, A. (1993). A New multi-category classification of subcutaneous fat deposits of songbirds (Una Nueva Clasificación, con Multi-categorías, para los Depósitos de Grasa en Aves Canoras). *J. F. Ornithol.* 64, 246–255.

Kaiser, S. A., Kershner, E. L., and Garcelon, D. K. (2009). "The influence of nest substrate and nest site characteristics on the risk of San Clemente sage sparrow nest failure," in *Proceedings of301the 7th California Islands Symposium* (Arcata, CA), 301–313.

Kamoske, A. G., Dahlin, K. M., Stark, S. C., and Serbin, S. P. (2019). Leaf area density from airborne LiDAR: comparing sensors and resolutions in a temperate broadleaf forest ecosystem. *For. Ecol. Manage.* 433, 364–375. doi: 10.1016/j.foreco.2018.11.017

Kleist, N. J., Guralnick, R., Cruz, A., Lowry, C., and Francis, C. (2018). Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. *Proc. Natl. Acad. Sci.* 115, E648–E657. doi: 10.1073/pnas.1709200115

LaZerte, S. E., Slabbekoorn, H., Otter, K. A., Francis, C., Ortega, C., Cruz, A., et al. (2016). Learning to cope: vocal adjustment to urban noise is correlated with prior experience in black-capped chickadees. *Proc. R. Soc. B* 283, e27052–e27052. doi: 10.1098/rspb.2016.1058

Lee, C., and MacDonald, J. (2011). *Baseline ambient sound levels in Point Reyes National Seashore*. (Los Angeles, CA: Department of Transportation, Western-Pacific Region).

Lee, C., and MacDonald, J. (2013). *Golden Gate National Recreation Area: Acoustical Monitoring 2007/2008*. (Fort Collins, CO: National Park service).

Liker, A., Papp, Z., Bókony, V., and Lendvai, Á. Z. (2008). Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. *J. Anim. Ecol.* 77, 789–795. doi: 10.1111/j.1365-2656.2008.01402.x

Luther, D., and Baptista, L. (2010). Urban noise and the cultural evolution of bird songs. *Proc. R. Soc. B* 277, 469–473. doi: 10.1098/rspb.2009.1571

Luther, D. A., Phillips, J., and Derryberry, E. P. (2016). Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. *Behav. Ecol.* 27, 332–340. doi: 10.1093/beheco/arv162

Manica, L. T., Maia, R., Dias, A., Podos, J., and Macedo, R. H. (2014). Vocal output predicts territory quality in a neotropical songbird. *Behav. Processes* 109, 21–26. doi: 10.1016/j.beproc.2014.07.004

Marzluff, J. M. (2017). A decadal review of urban ornithology and a prospectus for the future. *Ibis* 159, 1–13. doi: 10.1111/ibi.12430

Mazerolle, M. J. (2020). *AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c)*. R package version 2.3-0. Available online at: https://cran.r-project.org/package=AICcmodavg

McClintock, E. (2001). *The Trees of Golden Gate Park and San Francisco.* ed. R. G. J. Turner Berkeley (California, CA: Heydey Books).

Meillère, A., Brischoux, F., Parenteau, C., and Angelier, F. (2015). Influence of urbanization on body size, condition, and physiology in an urban exploiter: a multi-component approach. *PLoS ONE* 10:13568. doi: 10.1371/journal.pone.0135685

Morton, E. S. (1975). Ecological sources of selection on avian sounds. *Am. Nat.* 109, 17–34. doi: 10.1086/282971

Morton, M. L. (1992). Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the mountain white-crowned sparrow. *Condor* 94, 117–133. doi: 10.2307/1368802

Moseley, D. L., Lahti, D. C., and Podos, J. (2013). Responses to song playback vary with the vocal performance of both signal senders and receivers. *Proc. R. Soc. B* 280, 1–9. doi: 10.1098/rspb.2013.1401

Narango, D. L., and Rodewald, A. D. (2016). Urban-associated drivers of song variation along a rural-urban gradient. *Behav. Ecol.* 27, 608–616. doi: 10.1093/beheco/arv197

Narango, D. L., and Rodewald, A. D. (2018). Signal information of bird song changes in human-dominated landscapes. *Urban Ecosyst.* 21, 41–50. doi: 10.1007/s11252-017-0698-6

Ota, N., and Soma, M. (2014). Age-dependent song changes in a closed-ended vocal learner: elevation of song performance after song crystallization. *J. Avian Biol.* 45, 566–573. doi: 10.1111/jav.00383

Pärt, T., Arlt, D., Doligez, B., Low, M., and Qvarnström, A. (2011). Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. *J. Anim. Ecol.* 80, 1227–1235. doi: 10.1111/j.1365-2656.2011.01854.x

Pasch, B., George, A. S., Campbell, P., and Phelps, S. M. (2011). Androgen-dependent male vocal performance influences female preference in Neotropical singing mice. *Anim. Behav.* 82, 177–183. doi: 10.1016/j.anbehav.2011.04.018

Peig, J., and Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos* 118, 1883–1891. doi: 10.1111/j.1600-0706.2009.17643.x

Petrinovich, L., and Patterson, T. L. (1982). The white-crowned sparrow: stability, recruitment, and population structure in the Nuttall subspecies (1975-1980). *Auk* 99, 1–14. doi: 10.2307/4086016

Pettorelli, N., Laurance, W. F., O'brien, T. G., Wegmann, M., Nagendra, H., and Turner, W. (2014). Satellite remote sensing for applied ecologists: opportunities and challenges. *J. Appl. Ecol.* 51, 839–848. doi: 10.1111/1365-2664.12261

Phillips, J. N., Berlow, M., and Derryberry, E. P. (2018a). The effects of landscape urbanization on the gut microbiome: an exploration into the gut of urban and rural white-crowned sparrows. *Front. Ecol. Evol.* 6:148. doi: 10.3389/fevo.2018.00148

Phillips, J. N., and Derryberry, E. P. (2017a). Equivalent effects of bandwidth and trill rate: support for a performance constraint as a competitive signal. *Anim. Behav.* 132, 209–215. doi: 10.1016/j.anbehav.2017.08.012

Phillips, J. N., and Derryberry, E. P. (2017b). Vocal performance is a salient signal for male–male competition in white-crowned sparrows. *Auk* 134, 564–574. doi: 10.1642/AUK-17-2.1

Phillips, J. N., and Derryberry, E. P. (2018). Urban sparrows respond to a sexually selected trait with increased aggression in noise. *Sci. Rep.* 8:7505. doi: 10.1038/s41598-018-25834-6

Phillips, J. N., Gentry, K., Luther, D. A., and Derryberry, E. (2018b). Surviving in the City: higher apparent survivial for urban birds but worse condition on noisy territories. *Ecosphere* 9:e02440. doi: 10.1002/ecs2.2440

Phillips, J. N., and Katti, M. (2020). Anthropogenic noise affects winter song structure of a long distance migrant, Gambel's White-crowned Sparrow. *J. Urban Ecol.* 6, 1–9. doi: 10.1093/jue/juaa003

Phillips, J. N., Rochefort, C., Lipshutz, S., Derryberry, G. E., Luther, D., and Derryberry, E. P. (2020). Increased attenuation and reverberation are associated with lower maximum frequencies and narrow bandwidth of bird songs in cities. *J. Ornithol.* 161, 593–608. doi: 10.1007/s10336-020-01751-2

Pidgeon, A. M., Radeloff, V. C., and Mathews, N. E. (2006). Contrasting measures of fitness to classify habitat quality for the black-throated sparrow (*Amphispiza bilineata*). *Biol. Conserv.* 132, 199–210. doi: 10.1016/j.biocon.2006.03.024

Podos, J. (1996). Motor constraints on vocal development in a songbird. *Anim. Behav.* 51, 1061–1070. doi: 10.1006/anbe.1996.0107

Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* 51, 537–551. doi: 10.1111/j.1558-5646.1997.tb02441.x

Pyle, P. (1997). *Identification guide to North American birds*. Bolinas: Slate Creek Press.

R., Core Team, (2020). *R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing*. Available online at: https://www.R-project.org/

Robb, G. N., McDonald, R. A., Chamberlain, D. E., and Bearhop, S. (2008). Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.* 6, 476–484. doi: 10.1890/060152

Robert, J. H. (2020). *Raster: Geographic Data Analysis and Modeling*. R package version 3.3-7. Available online at: https://CRAN.R-project.org/package=raster

Rocchini, D., Boyd, D. S., Féret, J.-B., Foody, G. M., He, K. S., Lausch, A., et al. (2016). Satellite remote sensing to monitor species diversity: potential and pitfalls. *Remote Sens. Ecol. Conserv.* 2, 25–36. doi: 10.1002/rse2.9

Roughgarden, J., Running, S. W., and Matson, P. A. (1991). What does remote sensing do for ecology? *J. Ecol.* 72, 1918–1922. doi: 10.2307/1941546

Roussel, J.-R., David, A. (2018). *Airborne LiDAR Data Manipulation and Visualization for Forestry Applications*. Version 1.5.0.

Salmón, P., Nilsson, J. F., Nord, A., Bensch, S., and Isaksson, C. (2016). Urban environment shortens telomere length in nestling great tits, Parus major. *Biol. Lett.* 12, 254–260. doi: 10.1098/rsbl.2016.0155

Senar, J. C., Conroy, M. J., and Borras, A. (2002). Asymmetric exchange between populations differing in habitat quality: a metapopulation study on the citril finch. *J. Appl. Stat.* 29, 425–441. doi: 10.1080/02664760120108791

Shochat, E., Lerman, S., and Fernández-Juricic, E. (2010). Birds in urban ecosystems: population dynamics, community structure, biodiversity, and conservation. *Urban Ecosyst. Ecol. Agron. Monogr.* 55, 75–86. doi: 10.2134/agronmonogr55.c4

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., and Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.* 21, 186–191. doi: 10.1016/j.tree.2005.11.019

Slabbekoorn, H. (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* 85, 1089–1099. doi: 10.1016/j.anbehav.2013.01.021

Slabbekoorn, H., and den Boer-Visser, A. (2006). Cities change the songs of birds. *Curr. Biol.* 16, 2326–2331. doi: 10.1016/j.cub.2006.10.008

Slabbekoorn, H., Yeh, P., and Hunt, K. (2007). Sound transmission and song divergence : a comparison of urban and forest acoustics. *Condor* 109, 67–78. doi: 10.1093/condor/109.1.67

Smith, T. B., Harrigan, R. J., Kirschel, A. N. G., Buermann, W., Saatchi, S., Blumstein, D. T., et al. (2013). Predicting bird song from space. *Evol. Appl.* 6, 865–874. doi: 10.1111/eva.12072

Sprau, P., Roth, T., Amrhein, V., and Naguib, M. (2013). The predictive value of trill performance in a large repertoire songbird, the nightingale Luscinia megarhynchos. *J. Avian Biol.* 44, 567–574. doi: 10.1111/j.1600-048X.2013.00113.x

Swaddle, J. P., Francis, C. D., Barber, J. R., Cooper, C. B., Kyba, C. C. M., Dominoni, D. M., et al. (2015). A framework to assess evolutionary responses to anthropogenic light and sound. *Trends Ecol. Evol.* 30, 550–560. doi: 10.1016/j.tree.2015.06.009

van Oort, H., Otter, K. A., Fort, K. T., and Holschuh, C. I. (2006). Habitat quality, social dominance and dawn chorus song output in black-capped chickadees. *Ethology* 112, 772–778. doi: 10.1111/j.1439-0310.2006.01228.x

van Oort, H., Otter, K. A., Fort, K. T., and McDonell, Z. (2007). Habitat, dominance, and the phenotypic quality of male black-capped chickadees. *Condor* 109, 88–96. doi: 10.1093/condor/109.1.88

Ware, H. E., McClure, C. J. W., Carlisle, J. D., and Barber, J. R. (2015). A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. *Proc. Natl. Acad. Sci. USA*. 112:201504710. doi: 10.1073/pnas.1504710112

Wiley, R. H. (1991). Associations of song properties with habitats for territorial oscine birds of eastern North America. *Am. Nat.* 138, 973–993. doi: 10.1086/285263

Wilson, D. R., Bitton, P. P., Podos, J., and Mennill, D. J. (2014). Uneven sampling and the analysis of vocal performance constraints. *Am. Nat*. 183, 214–228. doi: 10.1086/674379

Yasukawa, K. (1979). Territory establishment in red-winged blackbirds: importance of aggressive behavior and experience. *Condor* 81, 258–264. doi: 10.2307/1367628

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OPINION
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How Should We Study Urban Speciation?

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Keywords: urban speciation, sexual selection, assortative mating, reproductive isolation, mating preferences, signal evolution

INTRODUCTION

Viewing cities as natural laboratories has great potential to improve our understanding of evolutionary processes. In the past two decades many studies revealed that urban individuals look, sound and behave differently than their non-urban counterparts (reviewed in Sol et al., 2013; Johnson and Munshi-South, 2017; Szulkin et al., 2020). These observations have led to the idea that urbanization can drive speciation and that cities can provide insight into the early stages of this process (Thompson et al., 2018).

Urbanization alters many natural and sexual selection pressures, a theoretical prerequisite for sympatric and parapatric modes of speciation (Kirkpatrick and Ravigné, 2002; van Doorn et al., 2004). Urban phenotypes may therefore represent the start of a new species, an exciting idea that allows us to study the mechanisms involved in the onset of speciation, rather than inferring any early-stage mechanisms from already existing (sub)species pairs. Urban speciation thus has the potential to advance the field of speciation research in general (Butlin et al., 2012). Unfortunately, we lack conclusive evidence of urban speciation at the moment. Many studies have revealed genetic divergence between urban and non-urban populations (reviewed in Johnson and Munshi-South, 2017), however in the face of ongoing geneflow, speciation also requires adaptive divergent selection between these populations (Servedio, 2004; Servedio et al., 2011; Verzijden et al., 2012).

Ecological speciation is the process by which new species form as a consequence of divergent natural or sexual selection pressures between contrasting environments (Nosil et al., 2016). For sexually reproducing organisms this process requires the evolution of assortative mating (= individuals from the same population mating more often than individuals from different populations). Assortative mating can operate via two separate routes: (1) any mechanism that causes individuals from the same population to be in the same location during the same time period; and (2) any mechanism that influences mate choice decisions. The first route is typically caused and influenced by natural selection pressures (e.g., adaptation to the "urban heat island" effect), the second route via sexual selection pressures (e.g., adaptation to increased competition over mates).

Here I would argue that we currently lack conclusive evidence that urban speciation is happening, despite many examples of genetic and phenotypic divergence, as well as some cases of assortative mating. For example, urban and non-urban populations may demonstrate differences in their sexual signals, but whether this divergence influences mating preferences has hardly been tested (Halfwerk et al., 2011). Furthermore, populations may adapt to urban conditions, but whether preferences for locally adapted mates will evolve depends on a genetic linkage between preferences and traits (Kirkpatrick and Ravigné, 2002; Maan and Seehausen, 2011; Butlin et al., 2012). Speciation may even be hampered by natural and sexual selection pressures associated with urbanization (Kirkpatrick and Nuismer, 2004).

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As most of the enthusiasm for urban speciation so far stems from studies that did not explicitly test for any of the crucial assumptions underlying its existence, I therefore call for more direct tests of some of the key components underlying the speciation process that may or may not occur in our cities. Below I discuss what evidence would justify to view cities as natural laboratories to study speciation and provide some examples of most promising study systems to search for it. I advocate that urban speciation most likely occurs and is strongly influenced when the conditions I outline below are met.

URBAN SPECIATION LIKELY FOLLOWS MODELS OF ECOLOGICAL SPECIATION

Speciation requires populations to become reproductively isolated, which can either be caused by a physical barrier between them (allopatric speciation) or by divergent selection on traits that favor assortative mating. Urban and non-urban populations can experience some level of isolation due to an increase in dispersal barriers, e.g., caused by roads or large areas of impervious surface. Urban populations can therefore evolve from non-urban populations via non-adaptive processes such as drift or founder effects (Perrier et al., 2018; Santangelo et al., 2018; Miles et al., 2019; Rivkin et al., 2019). For example, mosquitos in the London underground tunnels are genetically diverged from their above ground counterparts and this divergence is likely maintained by physical barriers (Byrne and Nichols, 1999). Most urban and non-urban populations would however experience substantial levels of geneflow between them and thus also require a mechanism of assortative mating to set them on the path toward becoming different species.

Ecological speciation models have been widely used to study how reproductive isolation can evolve in the face of ongoing geneflow and how evolutionary processes, such as adaptation, sexual selection, and speciation can influence one and other (Kirkpatrick and Ravigné, 2002; van Doorn et al., 2004; Rundle and Nosil, 2005; Maan and Seehausen, 2011). When trying to understand whether and how urban speciation evolves we can therefore rely to a large extent on theory and predictions derived from these models.

Urban speciation will likely (and probably only) occur under the following three conditions being present (*after* Kirkpatrick and Ravigné, 2002; Rundle and Nosil, 2005):

> (1) ecologically-based divergent selection on traits, (2) reproductive isolation, and (3) a (genetic) mechanism to link trait divergence (1) with isolation (2).

In short, for speciation to occur, urban and non-urban populations should experience divergent selection on specific traits and adaptively respond. The resulting trait divergence than either directly or indirectly initiates and drives assortative mating and thus over time increases reproductive isolation between the two populations. Divergent traits important for mate choice can e.g., directly increase assortative mating (Maan and Seehausen, 2011). Likewise, traits involved in habitat selection, or reproductive timing may directly influence when and where individuals from urban and non-urban populations meet. Adaptive changes to urbanization may also indirectly select for assortative mating. Reproductive isolation may for example evolve as a consequence of selection against non-adapted immigrants, although it is expected that such an indirect process would take more time than direct processes (Plath et al., 2010; Dominoni et al., 2013). Finally, the observed trait divergence and the direct or indirect link to assortative mating requires a mechanism to be maintained, which will most likely be genetic in nature (but see Danchin et al., 2018). As I will briefly review below, in many urban study systems, only one of these conditions has been assessed, or is currently met.

EVIDENCE FOR ECOLOGICALLY-BASED DIVERGENT SELECTION

An important step in urban speciation events involves divergent selection on traits that are directly or indirectly involved in reproductive isolation between urban and non-urban populations. Biotic and abiotic urban conditions can force populations to adapt specific ecological, phenological, physiological, morphological or behavioral traits. Many urban populations show e.g., higher tolerance to heat stress, suggesting selection has favored specific physiological traits (Campbell-Staton et al., 2020). Likewise, changes in predation risk may select for reduced or increased vigilance behavior, whereas changes in food availability may select for traits that alter competitiveness (Valcarcel and Fernández-Juricic, 2009; Halfwerk et al., 2019). Many other examples of adaptive responses to urbanization exist, see e.g., some of the research in this special issue, or some extensive reviews on urban adaptation and evolution (Johnson and Munshi-South, 2017; Szulkin et al., 2020). It is important to keep in mind that many of the observed differences between urban and non-urban individuals may however lack a genetic basis, and may therefore not be the best system (in particular the many vertebrate systems) to look for urban speciation, as not all three conditions might be met (see also below).

DOES ADAPTIVE URBAN EVOLUTION RESULT IN REPRODUCTIVE ISOLATION?

Adaptive changes in response to urbanization may directly or indirectly select for increased assortative mating between urban and non-urban populations. The direct route either involves divergent sexual selection on traits that function in sexual behavior, such as e.g., signals involved in inter- and intrasexual communication, or natural selection on traits involved in breeding decisions. Urban individuals could adapt breeding onset to increased temperatures, thereby reducing the temporal overlap with breeding individuals from non-urban populations, as has e.g., been found for blackbirds (Dominoni et al., 2013). Likewise, urban individuals may evolve specific habitat preferences thereby reducing the chance they encounter non-urban individuals.

Divergent selection on sexual traits mostly stem from studies on birdsong (Slabbekoorn, 2013). Urban acoustic conditions, in particular high levels of traffic sounds favor higher-pitched and louder songs as these suffer from less masking by the noise (Halfwerk and Slabbekoorn, 2009; Kunc and Schmidt, 2019). Many studies have reported urban birds to respond adaptively to noise by sing higher frequency songs, which can in turn directly influence mate choice (Halfwerk et al., 2011; Montague et al., 2013). Most examples involve however immediate signal flexibility, or developmental plasticity, and therefore do not provide the prerequisite of a genetic basis that links trait divergence to mate preferences. Such genetic basis may however evolve through a process of assimilation, assuming populations will maintain their phenotypic differences for long enough periods of time (Servedio, 2004; Danchin et al., 2018). Unfortunately, we lack evidence for assortative mating between urban and non-urban bird populations, as most studies only carried out playback experiments within one population, or used rival responses to song playback as indirect indicator (Ripmeester et al., 2010; Halfwerk et al., 2011). In other words, either the potential for reproductive isolation is unclear, or a genetic basis linking the song variation to this isolation is absent.

Reproductive isolation may also directly evolve via changes in temporal and spatial overlap between two divergent populations. Urban-adapted phenotypes may breed at other times or prefer to breed in specific locations, thereby increasing assortative mating through a simple chance process. Populations can e.g., adapt to the "urban heat island" effect by developing faster or starting to breed earlier (Dominoni et al., 2013). A similar process has already been reported for apple maggot flies which shifted hosts from hawthorn and consequently reduced temporal overlap between populations that inhabit the old host due to higher developmental temperatures in apples (Filchak et al., 2000).

Adaptive changes to urbanization may also indirectly select for assortative mating. Experimental evolution with lab populations suggest that selection for adaptive traits can increase reproductive isolation as a by-product (although tested in the absence of geneflow Rice and Hostert, 1993). Under field conditions, reproductive isolation may also evolve as a consequence of selection against non-adapted immigrants (Nosil et al., 2005). Urban individuals may for example not survive long enough outside the city to reproduce (and non-urban individuals *vice versa*), although that may seem somewhat extreme given the subtle differences that are often reported in urban studies. Alternatively, species may possess preferences for locally-adapted phenotypes, or evolve these preferences in response to urbanization. Females could for example prefer males that express condition-dependent secondary sexual traits (following a handicap-principle type of sexual selection model; Kirkpatrick and Ryan, 1991). The production of visual pigments involved in signaling is often constrained by a species' diet (e.g., red plumages of many bird species; Svensson and Wong, 2011). Locally-adapted individuals may differ in their feeding performance, influencing their visual displays, which can provide a basis for preference-based assortative mating between urban and non-urban populations. However, most studies focusing on condition-dependent signaling have so far reported that urban phenotypes are duller (Giraudeau et al., 2015).

ADAPTIVE EVOLUTION MAY HAMPER URBAN SPECIATION

Changes in urban-dependent selection pressures may not always enhance the likelihood of speciation (Candolin, 2009; Halfwerk et al., 2019; Sepp et al., 2020). For example, male tungara frogs (*Physaelemus pustulosus*) have increased their acoustic signal complexity in urban areas, presumably in response to increased competition over females as well as decreased risk of predation and parasitism (Halfwerk et al., 2019). Such adaptive response to changes in sexual selection can however constrain urban speciation (Kirkpatrick and Nuismer, 2004). In the tungara frog example, urban males have increased signal complexity, but when given a choice, females from both urban and forest populations preferred the urban phenotype. Sexual selection may in this case (and possibly many others) result in asymmetrical instead of decreased geneflow between populations.

DISCUSSION

In general, (more) studies on divergence in mate preference between urban and non-urban populations are highly needed. Divergent mating preferences may evolve in the absence of variation in the preferred traits, leading to a sensory-exploitation model of sexual selection and speciation (Kirkpatrick and Ryan, 1991). However, mating preferences are most likely to diverge in the presence of sexual trait divergence. In the absence of preference divergence, trait divergence may also lead to assortative mating, but probably only when mate choice is based on phenotypic similarity (e.g., in size, color or time of breeding; Maan and Seehausen, 2011). Assortative mating based on size might be a common mechanism driving speciation in cities. Studies could assess non-random mating in urban vs. non-urban populations based on size (or other traits), followed by mate choice trials in which the similarity trait can be experimentally manipulated (using e.g., video techniques, or robotics). Furthermore, clear cases of adaptive evolution in response to urbanization (e.g., heat tolerance, or adaptations to urban structures) are most prominent to test for the indirect evolution of assortative mating (either through mate choice test under common garden or divergent conditions). Finally, future studies should aim to integrate behavioral and genomic approaches to test for the prerequisite of reproductive isolation and the genetic mechanism(s) linking it to trait divergence, either through common garden breeding experiments to assess heritability, or genome-wide association studies to link genomic regions to divergent traits.

In conclusion, I argue that we currently lack any evidence of urban speciation, despite many examples of sexual behavior being influenced by a life in the city. In part this knowledge gap may be the result of the integrative approach that is required to conclusively show that urban and non-urban populations are locally adapted and on the path toward becoming separate species. Furthermore, most of our knowledge from the field comes from long-lived species, such as frogs and birds, that are difficult to track throughout their lives and often show a large extend of behavioral flexibility that can mask any underlying genetic mechanism. Bringing the lab to the field, or the field to the lab may help to unravel the mechanisms involved in urban speciation.

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REFERENCES

Butlin, R., Debelle, A., Kerth, C., Snook, R. R., Beukeboom, L. W., Cajas, R. F. C., et al. (2012). What do we need to know about speciation? *Trends Ecol. Evol.* 27, 27–39. doi: 10.1016/j.tree.2011.09.002

Byrne, K., and Nichols, R. A. (1999). Culex pipiens in London underground tunnels: differentiation between surface and subterranean populations. *Heredity* 82, 7–15. doi: 10.1038/sj.hdy.6884120

Campbell-Staton, S. C., Winchell, K. M., Rochette, N. C., Fredette, J., Maayan, I., Schweizer, R. M., et al. (2020). Parallel selection on thermal physiology facilitates repeated adaptation of city lizards to urban heat islands. *Nat. Ecol. Evol.* 4, 652–658. doi: 10.1038/s41559-020-1131-8

Candolin, U. (2009). Population responses to anthropogenic disturbance: lessons from three-spined sticklebacks Gasterosteus aculeatus in eutrophic habitats. *J. Fish Biol.* 75, 2108–2121. doi: 10.1111/j.1095-8649.2009.02405.x

Danchin, E., Nöbel, S., Pocheville, A., Dagaeff, A. C., Demay, L., Alphand, M., et al. (2018). Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science* 362, 1025–1030. doi: 10.1126/science.aat1590

Dominoni, D. M., Helm, B., Lehmann, M., Dowse, H. B., and Partecke, J. (2013). Clocks for the city: circadian differences between forest and city songbirds. *Proc. R. Soc. B Biol. Sci.* 280:20130593. doi: 10.1098/rspb.2013.0593

Filchak, K. E., Roethele, J. B., and Feder, J. L. (2000). Natural selection and sympatric divergence in the apple maggot Rhagoletis pomonella. *Nature* 407, 739–742. doi: 10.1038/35037578

Giraudeau, M., Mateos-Gonzalez, F., Cotín, J., Pagani-Nuñez, E., Torné-Noguera, A., and Senar, J. (2015). Metal exposure influences the melanin and carotenoid-based colorations in great tits. *Sci. Total Environ.* 532, 512–516. doi: 10.1016/j.scitotenv.2015.06.021

Halfwerk, W., Blaas, M., Kramer, L., Hijner, N., Trillo, P. A., Bernal, X. E., et al. (2019). Adaptive changes in sexual signalling in response to urbanization. *Nat. Ecol. Evol.* 3, 374–380. doi: 10.1038/s41559-018-0751-8

Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., ten Cate, C., et al. (2011). Low songs lose potency in urban noise conditions. *Proc. Natl. Acad. Sci. U.S.A.* 108, 14549–14554. doi: 10.1073/pnas.1109091108

Halfwerk, W., and Slabbekoorn, H. (2009). A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. *Anim. Behav.* 78, 1301–1307. doi: 10.1016/j.anbehav.2009.09.015

Johnson, M. T. J., and Munshi-South, J. (2017). Evolution of life in urban environments. *Science* 358:eaam8327. doi: 10.1126/science.aam8327

Kirkpatrick, M., and Nuismer, S. L. (2004). Sexual selection can constrain sympatric speciation. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 271, 687–693. doi: 10.1098/rspb.2003.2645

Kirkpatrick, M., and Ravigné, V. (2002). Speciation by natural and sexual selection: models and experiments. *Am. Nat.* 159, S22–S35. doi: 10.1086/338370

Kirkpatrick, M., and Ryan, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature* 350, 33–38. doi: 10.1038/350033a0

Kunc, H. P., and Schmidt, R. (2019). The effects of anthropogenic noise on animals: a meta-analysis. *Biol. Lett.* 15:20190649. doi: 10.1098/rsbl.2019.0649

Maan, M. E., and Seehausen, O. (2011). Ecology, sexual selection, and speciation. *Ecol. Lett.* 14, 591–602. doi: 10.1111/j.1461-0248.2011.01606.x

Miles, L. S., Rivkin, L. R., Johnson, M. T. J., Munshi-South, J., and Verrelli, B. C. (2019). Gene flow and genetic drift in urban environments. *Mol. Ecol.* 28, 4138–4151. doi: 10.1111/mec.15221

Montague, M. J., Danek-Gontard, M., and Kunc, H. P. (2013). Phenotypic plasticity affects the response of a sexually selected trait to anthropogenic noise. *Behav. Ecol.* 24, 342–348. doi: 10.1093/beheco/ars169

Nosil, P., Comeault, A., and Farkas, T. (2016). "Ecological speciation and its consequences," in *Encyclopedia of Evolutionary Biology*, ed R. M. Kliman, 487–493. doi: 10.1016/B978-0-12-800049-6.00067-6

Nosil, P., Vines, T. H., and Funk, D. J. (2005). Reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution* 59, 705–719. doi: 10.1111/j.0014-3820.2005.tb01747.x

Perrier, C. A., Lozano del Campo, A., Szulkin, M., Demeyrier, V., Gregoire, A., and Charmantier, A. (2018). Great tits and the city: distribution of genomic diversity and gene–environment associations along an urbanization gradient. *Evol. Appl.* 11, 593–613. doi: 10.1111/eva.12580

Plath, M., Riesch, R., Oranth, A., Dzienko, J., Karau, N., Schießl, A., et al. (2010). Complementary effect of natural and sexual selection against immigrants maintains differentiation between locally adapted fish. *Naturwissenschaften* 97, 769–774. doi: 10.1007/s00114-010-0691-x

Rice, W. R., and Hostert, E. E. (1993). Laboratory experiments on speciation: what have we learned in 40 years? *Evolution* 47, 1637–1653. doi: 10.1111/j.1558-5646.1993.tb01257.x

Ripmeester, E. A. P., Mulder, M., and Slabbekoorn, H. (2010). Habitat-dependent acoustic divergence affects playback response in urban and forest populations of the European blackbird. *Behav. Ecol.* 21, 876–883. doi: 10.1093/beheco/arq075

Rivkin, L. R., Santangelo, J. S., Alberti, M., Aronson, M. F., de Keyzer, C. W., Diamond, S. E., et al. (2019). A roadmap for urban evolutionary ecology. *Evol. Appl.* 12, 384–398. doi: 10.1111/eva.12734

Rundle, H. D., and Nosil, P. (2005). Ecological speciation. *Ecol. Lett.* 8, 336–352. doi: 10.1111/j.1461-0248.2004.00715.x

Santangelo, J. S., Rivkin, L. R., and Johnson, M. T. (2018). The evolution of city life. *Proc. Biol. Sci.* 285:20181529. doi: 10.1098/rspb.2018.1529

Sepp, T., McGraw, K. J., and Giraudeau, M. (2020). "Urban sexual selection," in *Urban Evolutionary Biology*, eds M. Szulkin, J. Munshi-South, and A. Charmantier, 234–252. doi: 10.1093/oso/9780198836841.003.0014

Servedio, M. R. (2004). The evolution of premating isolation: Local adaptation and natural and sexual selection against hybrids. *Evolution* 58, 913–924. doi: 10.1111/j.0014-3820.2004.tb00425.x

Servedio, M. R., Van Doorn, G. S., Kopp, M., Frame, A. M., and Nosil, P. (2011). Magic traits in speciation:'magic'but not rare? *Trends Ecol. Evol.* 26, 389–397. doi: 10.1016/j.tree.2011.04.005

Slabbekoorn, H. (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* 85, 1089–1099. doi: 10.1016/j.anbehav.2013.01.021

Sol, D., Lapiedra, O., and González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Anim. Behav.* 85, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Svensson, P. A., and Wong, B. (2011). Carotenoid-based signals in behavioural ecology: a review. *Behaviour* 148, 131–189. doi: 10.1163/000579510X548673

Szulkin, M., Munshi-South, J., and Charmantier, A. (2020). *Urban Evolutionary Biology*. New York, NY: Oxford University Press.

Thompson, K. A., Rieseberg, L. H., and Schluter, D. (2018). Speciation and the city. *Trends Ecol. Evol.* 33.11, 815–826. doi: 10.1016/j.tree.2018.08.007

Valcarcel, A., and Fernández-Juricic, E. (2009). Antipredator strategies of house finches: are urban habitats safe spots from predators even when humans are around? *Behav. Ecol. Sociobiol.* 63:673. doi: 10.1007/s00265-008-0701-6

van Doorn, G. S., Dieckmann, U., and Weissing, F. J. (2004). Sympatric speciation by sexual selection: a critical reevaluation. *Am. Nat.* 163, 709–725. doi: 10.1086/383619

Verzijden, M. N., ten Cate, C., Servedio, M. R., Kozak, G. M., Boughman, J. W., and Svensson, E. I. (2012). The impact of learning on sexual selection and speciation. *Trends Ecol. Evol.* 27, 511–519. doi: 10.1016/j.tree.2012.05.007

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Vigilance Response of a Key Prey Species to Anthropogenic and Natural Threats in Detroit

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Rapid urbanization coupled with increased human activity induces pressures that affect predator-prey relations through a suite of behavioral mechanisms, including alteration of avoidance and coexistence dynamics. Synergisms of natural and anthropogenic threats existing within urban environments exacerbate the necessity for species to differentially modify behavior to each risk. Here, we explore the behavioral response of a key prey species, cottontail rabbits (*Sylvilagus floridanus)*, to pressures from humans, domestic dogs, and a natural predator, coyotes (*Canis latrans*) in a human-dominated landscape. We conducted the first camera survey in urban parks throughout Detroit, Michigan in 2017–2020 to assess vigilance response corresponding to a heterogeneous landscape created from variation in the occupancy of threats. We predicted a scaled response where cottontail rabbits would be most vigilant in areas with high coyote activity, moderately vigilant in areas with high domestic dog activity, and the least vigilant in areas of high human activity. From 8,165 independent cottontail rabbit detections in Detroit across 11,616 trap nights, one-third were classified as vigilant. We found vigilance behavior increased with coyote occupancy and in locations with significantly high domestic dog activity, but found no significant impact of human occupancy or their spatial hotspots. We also found little spatial overlap between rabbits and threats, suggesting rabbits invest more in spatial avoidance; thus, less effort is required for vigilance. Our results elucidate strategies of a prey species coping with various risks to advance our understanding of the adaptability of wildlife in urban environments. In order to promote coexistence between people and wildlife in urban greenspaces, we must understand and anticipate the ecological implications of human-induced behavioral modifications.

Keywords: camera survey, domestic dog, anti-predator, cottontail rabbit, coyote, urban, occupancy

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INTRODUCTION

The 20th and 21st centuries have seen unprecedented population growth and expansion of cities, with 60% of the global population expected to live in urban centers by the year 2030 (United Nations, 2018). Urbanization coupled with other increased anthropogenic pressures has fundamentally changed ecosystems worldwide (Foley et al., 2005; Grimm et al., 2008;

Pickard et al., 2017; Chen et al., 2020). Cities fragment natural habitat and restrict gene flow, change species assemblages, and alter the behavior of animals and people alike (Romano, 2002; Tigas et al., 2002; Crooks et al., 2004; Lowry et al., 2013; Johnson and Munshi-South, 2017). These environmental perturbations have implications for wildlife and a myriad of ecological interactions including predator-prey relationships.

Non-consumptive fear effects induced by humans are pervasive in urban environments and drive behavioral changes in wildlife (Ciuti et al., 2012; Gaynor et al., 2018). For example, eastern gray squirrels (*Sciurus carolinensis*) in New York City have become sensitive to human movements and show behavioral plasticity in their ability to adjust flight initiation distance based on human activity (Bateman and Fleming, 2014). Exposure to human audio cues reduced foraging time and increased the amount of time spent being vigilant in badgers (*Meles meles*) in Great Britain as compared to exposure to non-human predator audio cues (Clinchy et al., 2016). Behavioral plasticity in predator and prey species alike directly influence their ability to avoid and coexist with intense human pressures in urban centers (Muhly et al., 2011; Lowry et al., 2013). While prey modify their behavior to avoid attempted predation, predators modify their behavior to account for prey behavior and to increase the likelihood of success of their predation attempts. Specifically, prey are forced to modify their behavior spatially or temporally to avoid threats from humans as well as associated domestic animals or natural predators (Fenn and Macdonald, 1995; Gliwicz and Dąbrowski, 2008; Reilly et al., 2017). Modification of behaviors have therefore become necessary for the survival of both predators and prey in urban environments, as risks govern behavior (Lima, 1998). However, despite the recent burgeoning of urban ecology studies, how humans and domestic animals alter mammalian vigilance behavior remains understudied.

Highly adaptable species and those with relatively smaller body sizes are more successful at coexisting with humans in urban areas (Bateman and Fleming, 2012). Carnivores, particularly large bodied carnivores, have historically faced intense persecution from humans (Bruskotter et al., 2017). Large predators depredate livestock and compete with humans for resources including space and prey, often resulting in humans employing lethal interventions (Mech, 1995; Witmer and Whittaker, 2001; Treves and Karanth, 2003; Muhly and Musiani, 2009). However, many mid to small-sized predators are able to thrive in areas of high anthropogenic influence (Wilkinson and Smith, 2001; Ikeda et al., 2004). In particular, coyotes (*Canis latrans*) have adapted to living with humans in part, by exploiting anthropogenic food subsidies and shifting diurnal movement in response to human disturbance (Kitchen et al., 2000; Gese and Beckoff, 2004). This, in conjunction with wide extirpations of the gray wolf (*Canis lupus*), has allowed coyotes to expand their range to the entirety of the United States beyond previous restrictions to the central and western portions of the country (Crooks and Soulé, 1999; Hody and Kays, 2018). Domestic dogs (*Canis familiaris)* have similarly become abundant within urban areas and thus, can exert top-down pressures as a member of the carnivore community (Ordeñana et al., 2010). These ecological and behavioral changes in carnivores can have cascading effects on their prey species, subsequently altering their behavior.

Concurrent with predators employing strategies for coexistence, their prey must also mitigate risks in human dominated landscapes. Threats for prey species in urban environments are often exacerbated by multiple sources including direct mortality from natural and anthropogenic sources. Prey may employ similar strategies to mitigate risks from humans as they do to mitigate risks from natural predators (Parsons et al., 2016). As such, fear effects in urban environments can result in prey modifying temporal activity or habitat selection to reduce predation risks (Chambers and Dickman, 2002; Dowding et al., 2010). Discernment between immediate and distal threats requires delegating time to vigilance in order to assess and respond to risks across the landscape. However, there are tradeoffs because more time spent being vigilant means less time foraging, mating, and performing other behaviors like grooming (Quenette, 1990). Environmental conditions including vegetation height, tree cover, and the distribution of water sources can interact to produce varying levels of predation risk and thus influence the amount of time prey spend being vigilant (Scheel, 1993; Tchabovsky et al., 2001).

Cottontail rabbits (*Sylvilagus floridanus*) are a key prey source for many mammalian carnivores as well as avian predators and occasionally snakes in urban environments throughout the United States (Beasom and Moore, 1977; Litvaitis and Shaw, 1980; Wittenberg, 2012). Because rabbits are an important part of coyotes' diet, along with small rodents, coyotes exert top-down pressures to control their populations (Poessel et al., 2017). Cottontail rabbits have high reproductive rates that result in rapidly growing populations that interact, directly or indirectly, with humans in gardens, yards, parks and other green spaces throughout city limits (Hunt et al., 2014; Baker et al., 2015). We conducted a non-invasive camera survey to investigate the vigilance behavior of rabbits in response to anthropogenic and natural threats. Our work occurred throughout Detroit, the largest city in Michigan, located in the Great Lakes region of the United States from 2017 to 2020. Here, we delineated human, coyote, and domestic dog risk zones to detect differences in cottontail vigilance response and investigated the potential factors influencing vigilance.

Species exploiting urban environments may exhibit higher plasticity to cope and acclimate with anthropogenic threats (Samia et al., 2015). The gray squirrel (*Sciurus carolinensis*), another common urban prey species, is less wary of humans in areas more densely populated by humans (Parker and Nilon, 2008). This suggests a level of acclimation to human presence, which we reasonably anticipate occurring in cottontail rabbits who are exposed to similar pressures of human activity in an urban environment. Therefore, we expect a similar level of acclimation in cottontail rabbits where they are less vigilant in areas heavily populated by humans. Because of the similarities in body size and behavior between domestic dogs and coyotes, we anticipate rabbits will show more vigilance in areas with high domestic dog presence than areas with high human presence.

However, domestic dog populations are generally larger in urban areas because of association with humans. In Detroit, we anticipate some level of acclimation to their presence from cottontail rabbits and therefore, we expect the response to dogs to be less dramatic than the response to coyotes. However, unaccompanied dogs could illicit pronounced fear responses. Overall, we expect a scaled response where rabbits will be least vigilant in areas with high human activity, with vigilance response increasing slightly in the areas with high domestic dog activity, and the most vigilance being displayed in areas of high coyote activity, as coyotes are an actual formidable predator of rabbits (**Figure 1**). Results will further our understanding of how a key prey species behaves in dynamic urban landscapes, information necessary to foster safe and positive interactions between people and wildlife coexisting in the city.

MATERIALS AND METHODS

Study Site

We implemented a systematic camera survey throughout metro parks in Detroit, the largest city in Michigan covering 359.2 km^2 of land (**Figure 2**). The declining city holds a human population of 672,000 people with an average density of ∼5,144 people per square mile (U.S. Census Bureau, 2016). The Detroit metro park system contributes to the green space and available habitat for wildlife within the city. All 28 total parks sampled within the city are impacted directly or indirectly by humans and are embedded within an urban matrix including roads, neighborhoods, and buildings. The parks range in size from ∼0.016 to 4.79 km^2 with varying levels of vegetation and human influence. In Detroit, the largest native carnivore present is the coyote. However, domestic dogs are also present and may exert pressures on the coyote's natural prey species such as rabbits.

Data Collection/Camera Survey

We deployed unbaited, remotely triggered cameras (Reconyx© PC 850, 850C, 900, 900C) throughout city parks to monitor the wildlife community from October – March in 2017–2020. Placement within the parks was determined based on evidence of wildlife presence such as scat, and vegetation type. Park size determined the number of cameras deployed, ranging from 1 to 7 cameras. For parks with multiple cameras, we deployed cameras with a minimum distance of 500 m between individual cameras. Cameras were affixed to medium sized trees approximately 0.5–1 m off the ground. We programmed cameras to take three images when triggered at high sensitivity with 1-s between each image and a 15-s quiet period. Every image was independently sorted and confirmed by at least two members of the Applied Wildlife Ecology Lab at the University of Michigan. We only used images confirmed as rabbit as well as their associated threat species of interests: humans, domestic dogs, and coyotes. Both gray (*Urocyon cinereoargenteus*) and red foxes (*Vulpes vulpes*) are also potential predators of cottontails, but sample sizes were too low to include in our analysis. Team members were excluded from human images.

Hotspot Analysis and Occupancy Modeling

To determine the level of risk from each of our three potential predator focal species, we used two methods to capture their spatial variation in parks across Detroit. First, we used kernel density analysis to construct utilization distributions from rabbit, human, coyote, and domestic dog camera triggers in

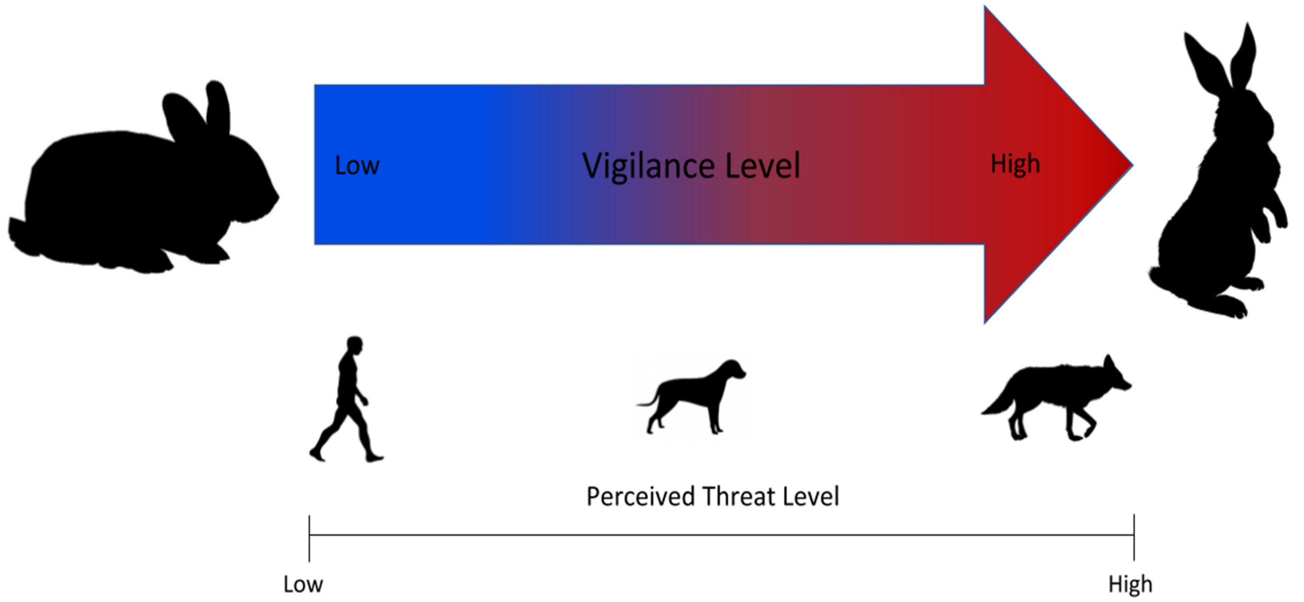

FIGURE 1 | Expected vigilance response of cottontail rabbits with scaled response across natural and anthropogenic threats.

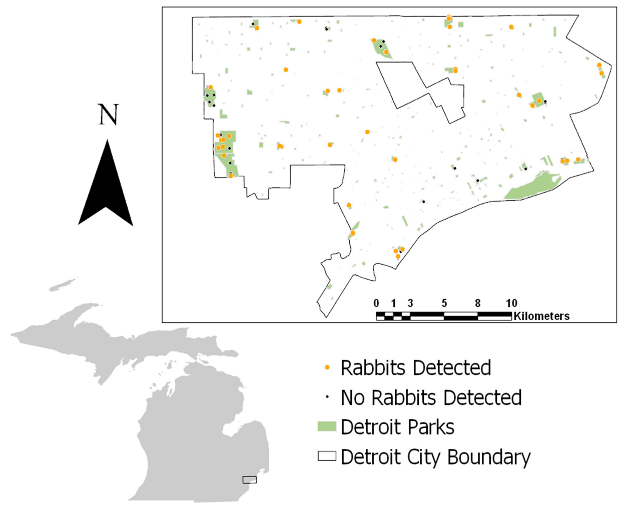

FIGURE 2 | Study site in Detroit with dots indicating camera placement from 2017 to 2020. Orange dots indicate camera stations where rabbits were detected in at least one of the years of study. Black dots indicate camera stations where no rabbits were detected in any years.

ArcMap (v. 10.6.1). To test for significant spatial clustering (i.e., hotspots), we applied the Getis-Ord GI* statistic to species triggers, which summarizes spatial autocorrelation with resultant high positive z-scores indicating clustering and low negative z-scores indicating dispersion (Getis and Ord, 1992). Specifically, significant trigger hotspots and coldspots are derived from z-scores greater than 1.96 and less than 1.96 ($\alpha < 0.05$), respectively. Finally, we overlaid significant trigger hotspots for rabbits with associated threats to determine if rabbits avoided hotspots for humans, dogs, or coyotes across the city. In other words, we assessed whether trigger hotspots for rabbits were congruent with any of the threats. Evidence of spatial avoidance may represent a sufficient evasion strategy that necessitates less vigilance behavior.

Second, we constructed single-species, single-season occupancy models for humans, domestic dog, and coyotes, which correct for imperfect detections from repeated surveys (MacKenzie et al., 2003; MacKenzie and Royle, 2005). In our case, we used 1-week sampling intervals to generate detection histories. By holding occupancy constant, we first built detection models with camera model (CAM), understory vegetation at camera (UAC), number of trap nights (TN), and park size (AREA) as covariates. We then used the top detection model to build occupancy models with housing density within 500 meters (HOUSE), prey trap success (PREYTS), UAC, and AREA. PREYTS was calculated at the camera level as the ratio of cottontail rabbit, squirrel, chipmunk (*Tamias striatus*), and small mammal total triggers by number of trap nights. We identified top models using Akaike's Information Criterion corrected for small sample sizes (AICc) based on the lowest Δ AIC and greatest weight (w). We also assessed goodness-of-fit for each model using the chi-squared discrepancy method in the "ResourceSelection" package. We constructed detection histories using "camtrapR," and completed occupancy modeling in "unmarked" packages. All analysis was completed in Program R.

Vigilance Scoring

We extracted behavioral information from images in order to quantify vigilance response in cottontail rabbits. For each image containing a rabbit, we scored vigilance based upon the position of the body and head (**Figure 3**). For images with two individuals, each individual was given its own classification and counted as independent from other individuals in the image. Rabbits were considered "vigilant" if their head was in an upright position; while "non-vigilant" was assigned when their head was down in a foraging position. For images where the rabbit did not display an obvious head up or head down stance, we used six other classifications: moving, active, eating, sniffing, out of frame, and unknown. "Moving" included any rabbit in motion, which was often indicated by motion blur in the images. We considered moving to be a potential indicator of vigilance as it could denote rabbits leaving an area due potentially to a detected threat. "Sniffing" included rabbit attention turned to monitoring an aspect of its environment with its head up such as sniffing twigs. Because we are investigating the impact of canid species on rabbit behavior and canids often mark their territory (Bowen and Cowan, 1980), we considered sniffing to potentially indicate vigilance as it is a show of risk assessment. Both sniffing and moving were left out of our initial vigilant vs. non-vigilant analysis but were included in the vigilant category in our extended analysis. "Active" was used for activity where the animal's attention was pointed inward at themselves. This included any rabbits scratching, licking, or otherwise attending to their fur, this also included stretching. "Eating" was used in the event that a rabbit had its head up, but clearly had vegetation in its mouth or the image series showed it chewing. Although both active and eating involve attention being pointed inward at the rabbit, we did not include them as non-vigilant in our analysis as we could not confirm non-vigilance. "Out of frame" included any images where the rabbit exited the frame of the picture and nothing was in the image. Images that were sorted as out of frame were removed from the data set and not counted in the final total. Finally, "unknown" was used for rabbits where only parts of the whole body were in the picture, the head was too blurry to determine, or if the body position could not be determined for any other reason. Unknown photos were also removed from the final total. Each individual was only designated one category per each image in which it appeared. All images with rabbits present were used to best estimate the amount of time actually spent in front of the camera at the particular station. We only used photos where rabbits were in the frame, meaning our photos are estimates of time spent in frame. Each image was scored independently for vigilance by at least two members of the Applied Wildlife Ecology Lab at the University of Michigan. Any discrepancies that were not resolved resulted in classifying the image as unknown.

We calculated multiple metrics of vigilance as a response variable to each risk factor. Initially, we used the raw number of images classified as vigilant per camera. Our second measure of vigilance was the ratio of vigilant photos to the total number of

FIGURE 3 | Vigilance classifications based on body position of cottontail rabbits: **(A)** vigilant, head-up; **(B)** non-vigilant, head down; **(C)** active; **(D)** eating; **(E)** moving; and **(F)** sniffing.

photos. This was used as a proxy for the relative amount of time spent being vigilant at each camera. For both these metrics, we started with just vigilant and non-vigilant and then expanded the classification of vigilant beyond head up versus head down and included moving and sniffing as vigilant. We used the total raw counts for these combined categories as well as the ratio of those categories out of the total number of detections as our "vigilant" response variable.

Statistical Analysis

We used negative binomial generalized linear models (GLM.nb) to determine which factors best-explained cottontail rabbit vigilance across cameras. We used results from the hotspot analysis to identify locations of significant high use based on kernel density estimates from detection data to categorize threat levels for humans, domestic dogs, and coyotes. This resulted in a binary explanatory variable indicating whether a hotspot was presence (1) or absence (0) for each threat. We also used occupancy estimates from top models for coyotes (COYO), humans (HUMO), and domestic dogs (DOGO) as threat covariates. We also included environmental and abiotic factors in our analysis. We calculated distance from each camera station to water sources (WATER), to roads (ROADS), and the area of each park (AREA, in acres) using ArcMap. We quantified understory cover (VEG) as a binary variable of whether trees, tall shrubs, bushes, or grasses were present or not in the field of view at the camera level.

Support for models was evaluated using Akaike's Information Criterion (AICc) to select top-performing model (Δ AIC < 2) with highest weight (*w*). We also assessed goodness-of-fit for each model using the chi-squared discrepancy method the "ResourceSelection" package. We completed modeling in the "lme4" package and model selection in the "MuMIn" package. All analysis was completed in Program R.

RESULTS

We obtained 8,165 cottontail rabbit detections from 58 camera locations in Detroit across 11,616 trap nights from our 2017–2020 surveys (**Table 1**). The average trap night per camera for the survey period was 99.8 (Range: 18–121) including two cameras which malfunctioned after 18 days, excluding the outliers the average was 101.2 (Range: 74–121). For parks with >1 camera station, cameras were spaced on average 1.4 km apart within parks spaced an average distance of 3.2 km apart. We recorded 1,345 human detections at 27 camera stations, 484 domestic

TABLE 1 | Number of detections for cottontail rabbits and associated threats tested that may influence their vigilance behavior in urban parks, Detroit Michigan 2017–2020.

Park	Rabbit	Human	Domestic Dog	Coyote
Balduck	495	22	44	0
Bishop	204	4	9	0
Butzel	2111	1	5	3
Chandler	18	3	7	7
Comstock	48	144	26	1
Conner	288	4	4	21
Eliza Howell	42	0	1	20
Farwell	325	47	31	1
Fields	28	25	36	0
Ford	259	8	32	6
Fort Wayne	1552	3	9	16
Hammerberg	120	0	2	1
Lasky	12	79	0	0
Maheras	102	7	4	29
Marruso	1005	21	77	0
McCabe	3	0	0	0
O'Hair	30	0	8	0
Palmer	42	7	8	8
Patton Memorial	557	28	3	26
Romanowski	75	7	0	0
Rouge	636	4	22	32
Stoepel #2	213	13	29	3

dog detections at 33 stations, and 271 coyote detections at 29 stations. Three stations (one in 2017 and two in 2019) had no coyote, domestic dog, or human detections. No cameras had significant trigger densities for all three threat species at the same station for the entire duration of study based on Getis-Ord Gi* statistics (**Figure 4**). Instead, coyotes had significantly high trigger densities to form a hotspot at only one station in 2019. Domestic dogs had hotspots at the same station across two different years. Humans had hotspots at three stations across the 3 years of study, with two of those stations recurring across years. Rabbits had significant trigger densities at the same two stations across 2 years. We found spatial aggregation of rabbits with dog at one hotspot location in 2 years. However, we saw no significant overlap in hotspots between rabbits and humans or coyotes (**Figure 4**).

Top occupancy models for all threats included HOUSE with PREYTS being important for both canid species (**Supplementary Table 1**). Detection models highlighted SIZE for all threats as important as well as TN, UAC, and CAM for humans and domestic dogs. Although comparable, estimates from top models indicated occupancy was highest for humans and lowest for coyotes throughout Detroit city parks ($\bar{\psi}_{\mathrm{HUMAN}} = 0.684$ SE = 0.057; $\bar{\psi}_{\mathrm{DOG}} = 0.662$ SE = 0.058; $\bar{\psi}_{\mathrm{COYOTE}} = 0.598$ SE = 0.061).

Of the rabbit detections, with vigilance being determined by head position, we categorized 2,774 images as vigilant (i.e., head-up, 34%) and 1,327 images as non-vigilant (i.e., head down, 16.3%). We classified the remaining 4,064 photos into the following categories: 17.4% moving, 1% active, 1.8% sniffing, and 1% eating. Over a quarter of the total images were either unknown or out of frame, with these categories both being removed from analysis.

Models further support differential effects of threats on rabbit vigilance (**Table 2**). The top model (highest w with Δ AIC < 2) indicated that the presence of domestic dog hotspots ($\beta = 2.63$, $p = 0.002$), coyote occupancy ($\beta = 0.869$, $p = 0.013$), vegetation cover ($\beta = 0.735$, $p = 0.031$) and distance to water ($\beta = 0.0001$, $p = 0.078$) all positively influenced vigilance, when the response variable represented was number of images with rabbits exhibited vigilance behavior. Though park size, roads, and human occupancy are in other top models, none of these variables had significant beta coefficients in explaining rabbit vigilance. Results of top models were consistent when using the extended categories of vigilance to include counts of moving and sniffing. The intercept-only model was included in top models when using ratio of vigilance photos. Therefore, we did not have sufficient power to investigate whether other variables explained the variation in the proportion of vigilant photos.

DISCUSSION

Urban wildlife must employ various behavioral strategies to cope with risks in their environment from naturogenic and anthropogenic sources (Stillfried et al., 2017; Blecha et al., 2018). Like other urban prey species, cottontail rabbits are facing predation threats that are dynamic in an increasingly urbanized world (Mccleery, 2009; Duarte and Young, 2011). We anticipated a scaled response where rabbits showed the lowest vigilance in areas of high human density, then progressively increased with in areas of high domestic dog density and even more in areas of high coyote density. Our analysis showed that occupancy of coyote positively influenced vigilance, consistent with expectations. We did find that rabbit vigilance behavior was heightened in hotspots of domestic dogs across the city. Further, consistent with our expectation, rabbit vigilance was not significantly affected by human occupancy suggesting more acclimation in a human-dominated landscape. Similarly, Gámez and Harris (in press) found no response of human occupancy on carnivore occupancy throughout Detroit in the same parks we surveyed here to access rabbit vigilance behavior. We also found that rabbit vigilance was significantly higher with more vegetation cover, which could be a response to lower visibility to detect predators.

While it is possible rabbits have acclimated to human presence (Samia et al., 2015; Dunagan et al., 2019), their response to domestic dogs indicates that they continue to perceive them as a threat. Domestic dogs are morphologically similar to coyotes, but occupy much higher densities in urban areas and may represent a novel threat similar enough to a natural predator to induce a stronger vigilance response. Coyotes may not occur above the density threshold required to induce behavioral modifications in rabbits in Detroit. Dogs may have functionally replaced coyotes in this capacity posing greater predation risk to cottontail rabbits. Similarly, vigilance behavior increased in

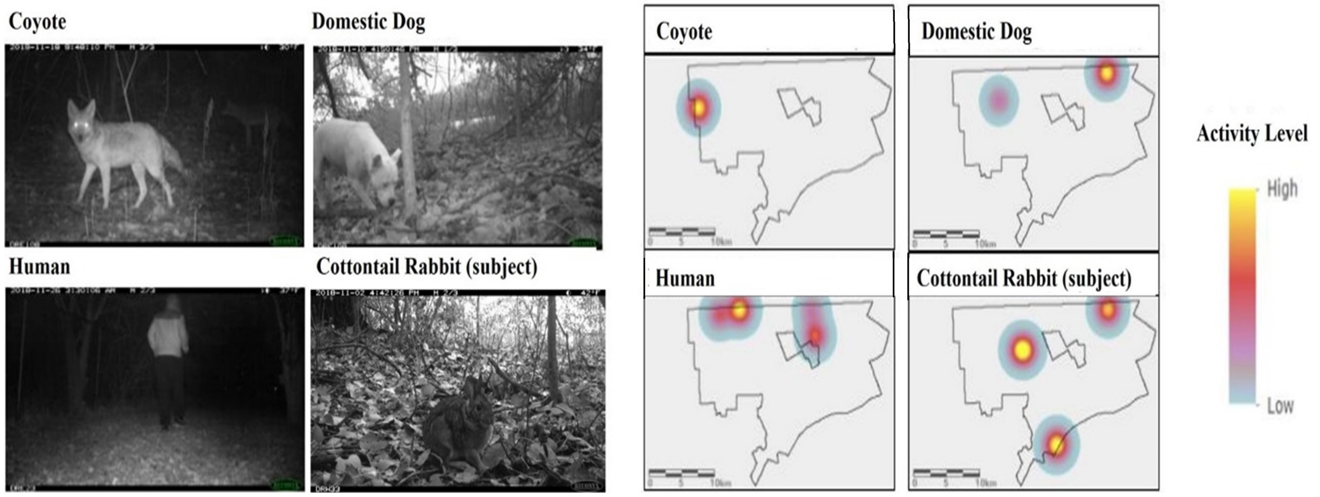

FIGURE 4 | Spatial use within Detroit for rabbits and their three threat species as shown by significant hotspots based on kernel density activity patterns from camera images in the city of Detroit parks from 2017 to 2020.

association with domestic dogs, but not coyotes in white-tailed deer (*Odocoileus virginianus*) in the mid-Atlantic region of the United States (Schuttler et al., 2017). Parsons et al. (2016) found that white-tailed deer and gray squirrel avoided humans with and without dogs more strongly than coyotes throughout the southeastern United States. Their findings were notably in contrast with other studies such as Parker and Nilon (2008) that suggested squirrels habituated to human activity in urban areas.

Ziege et al. (2016) found European rabbits (*Oryctolagus cuniculus*) were less vigilant in urban areas as compared to their counterparts in rural areas. This suggests that perhaps the important difference in vigilance lies in the urban-rural gradient, rather than entirely within the urban matrix. Similar to rural areas where there is more vegetation cover than urban areas, we found vigilance increased within areas with more vegetation cover. Rabbits occurring in areas with more vegetative cover increased their vigilance, which could indicate fear that the covered environment may obscure predators. In Missouri, Jones et al. (2016) reported that forest cover did not influence rabbit or squirrel occupancy across an urban-rural gradient study. We also found that as rabbits moved further away from water their vigilance level increased in the urban parks we sampled, which could reflect increased exposure to more developed areas in the urban matrix. Urban systems represent a novel landscape for rabbits that requires dynamic changes in vigilance based on the environment and threats of specific locations within the landscape.

TABLE 2 | Top models (<2 Δ AICc) that explained rabbit vigilance behavior using detection data from camera survey in Detroit city parks, 2017–2020.

Model	R^2	AICc	Δ AICc	*w*
COYO + DS + WATER + VEG	0.2535	553.7	0	0.210
COYO + DS + VEG	0.2109	554.5	0.73	0.146
COYO + DS + VEG + SIZE	0.2436	554.5	0.77	0.143
COYO + DS	0.1715	554.9	1.16	0.118
COYO + DS + VEG + ROAD	0.2364	555.1	1.32	0.109
COYO + DS + WATER	0.2011	555.2	1.44	0.102
COYO + DS + WATER + VEG + SIZE	0.2645	555.5	1.73	0.088
COYO + DS + WATER + VEG + HS	0.2629	555.6	1.86	0.083

Response variable is number of photos with rabbit head-up. Explanatory variables were: COYO (coyote occupancy), DS (presence of domestic dog hotspot), HS (presence of human hotspot), VEG (vegetation cover), WATER (distance to water), and SIZE (size of the park in acres). Model output for top models includes R^2, AICc, Δ AICc, and model weight (w).

Our hotspot analysis indicated very little spatial overlap between species, with domestic dogs and rabbits being the only two species to have significant densities at the same camera location in the same year. As a result, we conclude that generally, rabbits are investing more in spatial avoidance, requiring less effort for vigilance. By mostly avoiding their predators, rabbits may be better able to maintain constant levels of vigilance across the landscape rather than heightening vigilance in areas their predators occupy at significant densities. These hotspots of activity might also be confounded by other factors affecting vigilance that were not incorporated in our models. For example, rabbits might be selecting environments based on proximity to housing, overall vegetation density, or grass cover that might be less desirable for their predators, allowing the rabbits to spend less time being vigilant.

Notably, our analysis was limited in scope by only examining behavior in areas where these species co-occur. It is entirely possible that spatial or temporal partitioning plays a larger role in mediating predator-prey interactions than vigilance solely in prey. We examined interactions within patches in the city, but neglected to examine the amount of interaction occurring between these spaces. Quantifying the level of risks between patches in the city could be the next step in examining threat impacts on prey behavior. Furthermore, seasonality may influence vigilance behavior and interact with food availability (Périquet et al., 2017; Favreau et al., 2018). Our survey did not sample during warmer months. However, one could argue risk assessment in cottontail rabbits may be more extreme in the winter months when predators are more food-limited.

A growing number of studies on prey behavior have shown increasing evidence for multiple factors affecting predator prey dynamics including human influence and urbanization (Magle et al., 2014; Gallo et al., 2019). Our work contributes to the growing number of studies on urban wildlife and particularly predator-prey dynamics within urban systems. Further, we underscore that studying behavioral ecology across city topologies including cities where human populations are declining such as Detroit is necessary for understanding how humans, not just their built environment, affect wildlife to better promote coexistence between humans and wildlife (Guerrieri et al., 2012; Herrmann et al., 2016). Understanding the dynamics of predators and their prey in urban systems will be key to the continued coexistence of wildlife and humans in urban spaces. Our results elucidate how a common prey species changes, or fails to change, their vigilance behavior across anthropogenic and naturogenic risk factors in an urban ecosystem. Ultimately, these findings advance our understanding of the adaptability of wildlife in human-dominated environments.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

SL and NH conceived the study. SL wrote the manuscript and conducted analysis with support from SG and NH. SL and NA designed the graphics. NH secured funding and supervised work. All authors contributed to field efforts, data curation, and editing the manuscript.

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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.2021.570734/full#supplementary-material

REFERENCES

Baker, M. A. A., Emerson, S. E., and Brown, J. S. (2015). Foraging and habitat use of eastern cottontails (*Sylvilagus floridanus*) in an urban landscape. *Urban Ecosystems* 18, 977–987. doi: 10.1007/s11252-015-0463-7

Bateman, P. W., and Fleming, P. A. (2012). Big city life: carnivores in urban environments. *J. Zool.* 287, 1–23. doi: 10.1111/j.1469-7998.2011.00887.x

Bateman, P. W., and Fleming, P. A. (2014). Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *J. Zool.* 294, 93–98. doi: 10.1111/jzo.12156

Beasom, S. L., and Moore, R. A. (1977). Bobcat food habit response to a change in prey abundance. *Southwestern Nat.* 21, 451–457.

Blecha, K. A., Boone, R. B., and Alldredge, M. W. (2018). Hunger mediates apex predator's risk avoidance response in wildland–urban interface. *J. Anim. Ecol.* 87, 609–622. doi: 10.1111/1365-2656.12801

Bowen, W. D., and Cowan, I. M. (1980). Scent marking in coyotes. *Can. J. Zool.* 58, 473–480. doi: 10.1139/z80-065

Bruskotter, J. T., Vucetich, J. A., Manfredo, M. J., Karns, G. R., Wolf, C., Ard, K., et al. (2017). Modernization, risk, and conservation of the world's largest carnivores. *BioScience* 67, 646–655. doi: 10.1093/biosci/bix049
Note - 11 authors https://doi.org/10.1093/biosci/bix049

Chambers, L. K., and Dickman, C. R. (2002). Habitat selection of the long-nosed bandicoot, *Perameles nasuta* (*Mammalia, Peramelidae*), in a patchy urban environment. *Austral Ecol.* 27, 334–342. doi: 10.1046/j.1442-9993.2002.t01-1-01185.x

Chen, G., Li, X., Liu, X., Chen, Y., Liang, X., Leng, J., et al. (2020). Global projections of future urban land expansion under shared socioeconomic pathways. *Nat. Commun.* 11:537.

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., et al. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS One* 7:e50611. doi: 10.1371/journal.pone.0050611

Clinchy, M., Zanette, L. Y., Roberts, D., Suraci, J. P., Buesching, C. D., Newman, C., et al. (2016). Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. *Behav. Ecol.* 27, 1826–1832.

Crooks, K. R., and Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400, 563–566. doi: 10.1038/23028

Crooks, K. R., Suarez, A. V., and Bolger, D. T. (2004). Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biol. Conserv.* 115, 451–462. doi: 10.1016/s0006-3207(03)00162-9

Dowding, C. V., Harris, S., Poulton, S., and Baker, P. J. (2010). Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus*, in relation to risk and reward. *Anim. Behav.* 80, 13–21. doi: 10.1016/j.anbehav.2010.04.007

Duarte, M. H., and Young, R. J. (2011). Sleeping site selection by urban marmosets (*Callithrix penicillata*) under conditions of exceptionally high predator density. *Int. J. Primatol.* 32, 329–334. doi: 10.1007/s10764-010-9468-5

Dunagan, S. P., Karels, T. J., Moriarty, J. G., Brown, J. L., and Riley, S. P. D. (2019). Bobcat and rabbit habitat use in an urban landscape. *J. Mammol.* 100, 401–409. doi: 10.1093/jmammal/gyz062

Favreau, F., Goldizen, A. W., Fritz, H., and Pays, O. (2018). Food supply fluctuations constrain group sizes of kangaroos and in turn shape their vigilance and feeding strategies. *Anim. Behav.* 135, 165–176. doi: 10.1016/j.anbehav.2017.11.020

Fenn, M. G., and Macdonald, D. W. (1995). Use of middens by red foxes: risk reverses rhythms of rats. *J. Mammal.* 76, 130–136. doi: 10.2307/1382321

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., et al. (2005). Global consequences of land use. *Science* 309, 570–574. doi: 10.1126/science.1111772

Gallo, T., Fidino, M., Lehrer, E. W., and Magle, S. (2019). Urbanization alters predator-avoidance behaviours. *J. Anim. Ecol.* 88, 793–803. doi: 10.1111/1365-2656.12967

Gámez, S., and Harris, N. C. (in press). Living in the concrete jungle:(carnivore)spatial ecology in urban parks. *Ecol. Appl.*

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., and Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science* 360, 1232–1235. doi: 10.1126/science.aar7121

Gese, E. M., and Beckoff, M. (2004). "Coyote *Canis Latrans*," in *Canids: Foxes, Wolves, Jackals, and Dogs: Status Survey and Conservation Action Plan*, eds C. Sillero-Zubiri, M. Hoffmann, and D. W. Macdonald (Gland: IUCN).

Getis, A., and Ord, J. K. (1992). The analysis of spatial association. *Geograph. Anal.* 24, 189–206.

Gliwicz, J., and Dąbrowski, M. J. (2008). Ecological factors affecting the diel activity of voles in a multi-species community. *Annal. Zool. Fennici* 45, 242–247. doi: 10.5735/086.045.0401

Grimm, N. B., Foster, D., Groffman, P., Grove, J. M., Hopkinson, C. S., et al. (2008). The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. *Front. Ecol. Environ.* 6:264–272. doi: 10.1890/070147

Guerrieri, V., Hartley, D., and Hurst, E. (2012). Within-City variation in urban decline: the case of detroit. *Am. Econom. Rev.* 102, 120–126. doi: 10.1257/aer.102.3.120

Herrmann, D. L., Schwarz, K., Shuster, W. D., Berland, A., Chaffin, B. C., Garmestani, A. S., et al. (2016). Ecology for the Shrinking City. *Bioscience* 66, 965–973.

Hody, J. W., and Kays, R. (2018). Mapping the expansion of coyotes (*Canis latrans*) across North and Central America. *ZooKeys* 759, 81–97. doi: 10.3897/zookeys.759.15149

Hunt, V. M., Magle, S. B., Vargas, C., Brown, A. W., Lonsdorf, E. V., et al. (2014). Survival, abundance, and capture rate of eastern cottontail rabbits in an urban park. *Urban Ecosystems* 17, 547–560. doi: 10.1007/s11252-013-0334-z

Ikeda, T., Asano, M., Matoba, Y., and Abe, G. (2004). Present status of invasive alien raccoon and its impact in Japan. *Global Environ. Res.* 8, 125–131.

Johnson, M. T., and Munshi-South, J. (2017). Evolution of life in urban environments. *Science* 358:eaam8327. doi: 10.1126/science.aam8327

Jones, B. M., Cove, M. V., Lashley, M. A., and Jackson, V. L. (2016). Do coyotes *Canis latrans* influence occupancy of prey in suburban forest fragments? *Curr. Zool.* 62, 1–6. doi: 10.1093/cz/zov004

Kitchen, A. M., Gese, E. M., and Schauster, E. R. (2000). Changes in coyote activity patterns due to reduced exposure to human persecution. *Can. J. Zool.* 78, 853–857. doi: 10.1139/z00-003

Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48, 25–34. doi: 10.2307/1313225

Litvaitis, J. A., and Shaw, J. H. (1980). Coyote movements, habitat use, and food habits in southwestern Oklahoma. *J. Wildlife Manag.* 44, 62–68. doi: 10.2307/3808351

Lowry, H., Lill, A., and Wong, B. B. (2013). Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549. doi: 10.1111/brv.12012

MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., and Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207. doi: 10.1890/02-3090

MacKenzie, D. I., and Royle, J. A. (2005). Designing occupancy studies: general advice and allocating survey effort. *J. Appl. Ecol.* 42, 1105–1114. doi: 10.1111/j.1365-2664.2005.01098.x

Magle, S. B., Simoni, L. S., Lehrer, E. W., and Brown, J. S. (2014). Urban predator–prey association: coyote and deer distributions in the Chicago metropolitan area. *Urban Ecosystems* 17, 875–891. doi: 10.1007/s11252-014-0389-5

Mccleery, R. A. (2009). Changes in fox squirrel anti-predator behaviors across the urban–rural gradient. *Landscape Ecol.* 24, 483–493. doi: 10.1007/s10980-009-9323-2

Mech, L. D. (1995). The challenge and opportunity of recovering wolf populations. *Conserv. Biol.* 9, 270–278. doi: 10.1046/j.1523-1739.1995.9020270.x

Muhly, T. B., and Musiani, M. (2009). Livestock depredation by wolves and the ranching economy in the Northwestern US. *Ecol. Econom.* 68, 2439–2450. doi: 10.1016/j.ecolecon.2009.04.008

Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L., and Musiani, M. (2011). Human activity helps prey win the predator-prey space race. *PLoS One* 6:e17050. doi: 10.1371/journal.pone.0017050

Ordeñana, M. A., Crooks, K. R., Boydston, E. E., Fisher, R. N., Lyren, L. M., et al. (2010). Effects of urbanization on carnivore species distribution and richness. *J. Mammol.* 91, 1322–1331. doi: 10.1644/09-mamm-a-312.1

Parker, T. S., and Nilon, C. H. (2008). Gray squirrel density, habitat suitability, and behavior in urban parks. *Urban Ecosystems* 11, 243–255. doi: 10.1007/s11252-008-0060-0

Parsons, A. W., Bland, C., Forrester, T., Baker-Whatton, M. C., Schuttler, S. G., McShea, W. J., et al. (2016). The ecological impact of humans and dogs on wildlife in protected areas in eastern North America. *Biol. Conserv.* 203, 75–88. doi: 10.1016/j.biocon.2016.09.001

Périquet, S., Richardson, P., Cameron, E. Z., Ganswindt, A., Belton, L., Loubser, E., et al. (2017). Effects of lions on behaviour and endocrine stress in plains zebras. *Ethology* 123, 667–674. doi: 10.1111/eth.12638

Pickard, B. R., Van Berkel, D., Petrasova, A., and Meentemeyer, R. K. (2017). Forecasts of urbanization scenarios reveal trade-offs between landscape change and ecosystem services. *Landscape Ecol.* 32, 617–634. doi: 10.1007/s10980-016-0465-8

Poessel, S. A., Mock, E. C., and Breck, S. W. (2017). Coyote (*Canis latrans*) diet in an urban environment: variation relative to pet conflicts, housing density, and season. *Can. J. Zool.* 95, 287–297. doi: 10.1139/cjz-2016-0029

Quenette, P. Y. (1990). Functions of vigilance behaviour in mammals: a review. *Acta Oecol.* 11, 801–818.

Reilly, M. L., Tobler, M. W., Sonderegger, D. L., and Beier, P. (2017). Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. *Biol. Conserv.* 207, 117–126. doi: 10.1016/j.biocon.2016.11.003

Romano, B. (2002). "Evaluation of urban fragmentation in the ecosystems," in *Proceedings of International Conference on Mountain Environment and Development (ICMED)*, (Chengdu), 15–19.

Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F., and Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. *Nat. Commun.* 6:8877.

Scheel, D. (1993). Watching for lions in the grass: the usefulness of scanning and its effects during hunts. *Anim. Behav.* 46, 695–704. doi: 10.1006/anbe.1993.1246

Schuttler, S. G., Parsons, A. W., Forrester, T. D., Baker, M. C., McShea, W. J., Costello, R., et al. (2017). Deer on the lookout: how hunting, hiking and coyotes affect white-tailed deer vigilance. *J. Zool.* 301, 320–327. doi: 10.1111/jzo.12416

Stillfried, M., Gras, P., Börner, K., Göritz, F., Painer, J., et al. (2017). Secrets of success in a landscape of fear: urban wild boar adjust risk perception and tolerate disturbance. *Front. Ecol. Evol.* 5:157. doi: 10.3389/fevo.2017.00157

Tchabovsky, A. V., Krasnov, B., Khokhlova, I. S., and Shenbrot, G. I. (2001). The effect of vegetation cover on vigilance and foraging tactics in the fat sand rat Psammomys obesus. *J. Ethol.* 19, 105–113. doi: 10.1007/s101640170006

Tigas, L. A., Van Vuren, D. H., and Sauvajot, R. M. (2002). Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biol. Conserv.* 108, 299–306. doi: 10.1016/s0006-3207(02)00120-9

Treves, A., and Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.* 17, 1491–1499. doi: 10.1111/j.1523-1739.2003.00059.x

United Nations (2018). *World Urbanization Prospects - Population Division*. New York, NY: United Nations.

U.S. Census Bureau (2016). *Decennial Census of Population and Housing*. Suitland, MD: U.S. Census Bureau.

Wilkinson, D., and Smith, G. C. (2001). A preliminary survey for changes in urban fox (*Vulpes vulpes*) densities in England and Wales, and implications for rabies control. *Mammal Rev.* 31, 107–110. doi: 10.1046/j.1365-2907.2001.00076.x

Witmer, G. W., and Whittaker, D. G. (2001). *Dealing with Nuisance and Depredating Black Bears*. Londonderry: USDA National Wildlife Research Center-Staff Publications, 581.

Wittenberg, R. D. (2012). Foraging ecology of the timber rattlesnake (Crotalus horridus) in a fragmented agricultural landscape. *Herpetol. Conserv. Biol.* 7, 449–461.

Ziege, M., Babitsch, D., Brix, M., Kriesten, S., Straskraba, S., et al. (2016). Extended diurnal activity patterns of European rabbits along a rural-to-urban gradient. *Mammal. Biol.* 81, 534–541. doi: 10.1016/j.mambio.2016.07.002

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Incubation Behavior Differences in Urban and Rural House Wrens, *Troglodytes aedon*

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As global land surfaces are being converted to urban areas at an alarming rate, understanding how individuals respond to urbanization is a key focus for behavioral ecology. As a critical component of avian parental care, incubating adults face a tradeoff between maintaining an optimal thermal environment for the developing embryos while meeting their own energetic demands. Urban habitats are biotically and abiotically different from their rural counterparts, *i.e.*, in food availability, predator compositions, and the thermal environment. Therefore, urban birds may face different incubation challenges than their natural counterparts. We measured incubation behavior of rural and urban house wrens, *Troglodytes aedon*, with temperature loggers throughout the 12-day period. We found that urban females had more incubation bouts of shorter duration and spent less total time incubating per day than rural females. Results could provide evidence of behavioral shifts of wrens in cities, which have implications for the evolution of parental care. Our findings contribute to our understanding of the behavioral traits needed for city life and possible environmental pressures driving urban adaptations.

Keywords: behavioral flexibility, heat island, food availability, parental care, plasticity, avian reproduction, anthropogenic effects, thermal buttons

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INTRODUCTION

The growth and spread of urban areas is one of the most extensive of all anthropogenic effects (Johnson and Munshi-South, 2017). Landscapes are rapidly changing to become more urbanized (Chen et al., 2020), and these effects are expected to exponentially increase as more than two-thirds of the world's population is projected to live in urban areas by 2050 (United Nations, 2018). Urban environments present a unique set of challenges to wildlife which have led to changes in wildlife behavior, physiology, morphology, and fitness (Hall and Warner, 2018; Ouyang et al., 2019; Reynolds et al., 2019). Despite urban environmental challenges, some species continue to colonize and thrive in urban environments (urban exploiters; Sepp et al., 2018). Understanding how and why urban exploiters thrive in urban environments is a major goal in evolutionary ecology (Ouyang et al., 2018). Avian systems are ideal to study effects of urbanization, as their behavior is easily observed, they readily colonize new habitats, and can act as bioindicators of urban pollutants (Bonier et al., 2007; Zhang and Ma, 2011; Sol et al., 2013; Marzluff, 2017).

Behavioral flexibility and innovation represent the first line of defense against novel challenges (Mckinney, 2002, 2006; Shochat et al., 2006; Sih et al., 2011; Sol et al., 2013). Environmental alterations in cities, such as reduced and fragmented natural vegetation, novel building structures, human disturbance, new predator compositions, and elevated light, noise and heavy metal pollution, can all affect behavioral phenotypes of urban adapters (Gorissen et al., 2005; Shochat et al., 2010; Clucas and Marzluff, 2012; Sol et al., 2013; Seress and Liker, 2015). The urban heat island, for example, is a phenomenon in which cities are several degrees hotter than the natural environments from which they are built (Landsberg, 1981; Arnfield, 2003; Peng et al., 2012). Urban habitats may also have lower food availability for avian wildlife, especially in nutritious food for insectivorous birds (Seress et al., 2018, 2020; Baldan and Ouyang, 2020). Furthermore, predator compositions can vary across the urban-rural gradient and between artificial and natural nests (Rodewald and Kearns, 2011; Vincze et al., 2017; Eötvös et al., 2018). Studying behavioral differences between urban wildlife and their natural counterparts gives us the opportunity to understand the environmental pressures driving adaptations needed for urban living.

While wildlife have shifted life history traits to compensate for changes in their environments, important aspects of avian parental care that ensure embryonic development, such as incubation, may be affected as well. For eggs to successfully hatch, the egg-adult unit in contact incubation is critical (Deeming, 2002c). An essential aspect of avian parental care is behaviorally maintaining and creating a thermal environment suitable for offspring development (Skutch, 1962; Deeming, 2002b). Avian embryos require a narrow species-specific thermal range for optimal development in which any prolonged period outside the limits result in embryonic development abnormalities (reviewed in Durant et al., 2013). Even small variations in the thermal environment can influence offspring phenotypes, such as growth rate, immune function, and survival (Pérez et al., 2008; Ardia et al., 2010; Nord and Nilsson, 2011; Durant et al., 2013; Ospina, 2017; Merrill et al., 2020).

Furthermore, female-only incubation is especially constrained (Deeming, 2002b; Nord and Williams, 2015). The length and frequency of female incubation behavior are affected by ambient temperature, food availability, and presence of predators (Skutch, 1962; Conway and Martin, 2000a,b; Londoño et al., 2008). Seeing as these abiotic and biotic factors also differ between urban and rural areas, incubating adults should adjust their incubation strategies to maintain optimal embryonic development in the face of urban environmental changes. Behavioral adjustments in incubation, such as more and shorter bouts, can lead to reduced attentiveness and have been reported when adults are exposed to elevated ambient temperatures in both experimental (Ton et al., 2021) and field studies (Haftorn, 1979; Conway and Martin, 2000a; Londoño et al., 2008; Álvarez and Barba, 2014; McClintock et al., 2014; Amininasab et al., 2016; Batisteli et al., 2020). Elevated risk of predation has been shown to lengthen both incubation and recess bouts so as to decrease activity at the nest (Martin and Ghalambor, 1999; Conway and Martin, 2000b). Additionally, low food abundance may increase the energetic expense of foraging trips and result in more frequent and longer recesses (Conway and Martin, 2000b; Londoño et al., 2008). Therefore, the incubation life history stage requires the female to face a tradeoff between maintaining her own energetic needs, *e.g.*, self-maintenance, and maintaining an optimal thermal environment during incubation (Conway and Martin, 2000a; Deeming, 2002a). With avian incubation tightly linked to various climactic conditions, these behaviors are critically sensitive to climate changes (Mainwaring, 2015).

It is likely that a variety of urban factors will affect incubation behaviors, leading to differences in offspring development and/or energy balance in the female. However, there are currently no studies that we are aware of that have investigated differences in incubation strategies between urban and non-urban birds. Here, we used thermal buttons in nests of both urban and rural house wrens (*Troglodytes aedon*) to test whether their strategies would differ and if these differences match the trends in their thermal environments. House wrens are small cavity nesters that readily use nest boxes in both urban and rural locations with female only incubation (Ouyang et al., 2019). Whether due to less food availability, increased thermal environment or decreased natural predators in the urban environment, we predicted that incubation bouts would be shorter in urban birds. Overall, we predicted that due to the combined factors of the urban environment, female wrens would spend less time on the nest incubating eggs compared to rural wrens.

MATERIALS AND METHODS

Study Site Descriptions

This study was conducted from May to August 2019 at one urban location in Reno, NV, United States, and one rural location in Sparks, NV, United States. The urban site was a city park (39°30′3″N, 119°50′ 00″W) and the rural site was at the University of Nevada, Reno Agricultural Experimental Station, a university owned agricultural farm (39°30′ 50″N, 119°51′ 43″W). These two sites differed in urbanization score and environmental traits (see Baldan and Ouyang, 2020 for a detailed description of the field sites). Briefly, an urbanization score was estimated following the validated methods of Seress et al. (2014) in which land use was estimated by scoring vegetation abundance, building density, and paved surfaces from aerial images of each site composed of 100 × 100 m cells. The urban site has a higher urbanization score compared to the rural site with more cells containing increased building density and paved surfaces as well as decreased vegetation density (Baldan and Ouyang, 2020).

Incubation Behavior

We checked nest boxes daily to monitor nest building, egg laying, and initiation of incubation ($x = 8$ urban, 7 rural nests). On the first day of incubation, determined as the first day no further egg was laid and eggs felt warm to the touch, we placed an iButton temperature logger (Model Thermochron TCS, OnSolution, Baulkham Hills, New South Wales, Australia; accuracy: ±0.5°C, resolution: 0.5°C) within the center of the nest cup among the eggs. iButtons were placed in the same location in the nest cup and remained for the entire duration of incubation until chicks hatched. No iButtons were found moved or removed. We also measured ambient temperature at our sites using iButtons. Two ambient iButtons were attached to the outer underside of two nest boxes at each site evenly spaced out from one another across the site. We validated these temperatures with weather stations located near our sites. At the urban site, the weather station was 0.67 km from the location of our boxes (Weather Underground, Southwest Reno – KNVRENO251) and at the rural site, the weather station was located at the breeding site [Western Regional Climate Center – Desert Research Institute – Reno, Nevada, Sparks (UNR) Nevada].

Maternal incubation behavior was measured from a time series of temperature data collected by iButton temperature data loggers (Cooper and Mills, 2005). iButtons have been previously shown to accurately measure incubation and recess bouts of female incubation behavior (Nord and Cooper, 2019). Temperature loggers recorded a temperature measurement every 2 min throughout the entire 12-day incubation period.

We used the combination of both Rhythm and Raven Pro software programs (Cooper and Mills, 2005) to compute incubation bouts and duration while taking ambient temperatures into account. We analyzed daytime incubation behavior determined by daily sunrise and sunset times and included days 2 through 11 of the 12-day incubation period to ensure analysis of only full incubation days (there was no individual variation in incubation period: all birds had an incubation period of 12 days). The Rhythm program (1.1, Cooper and Mills, 2005) was used to identify incubation bouts and recesses considering a bout as a rise in nest temperature of more than 2°C with the rise in temperature trend lasting more than 2 min (Amininasab et al., 2016). We used the Raven Pro program (1.6, Cooper and Mills, 2005) to visually inspect the selected bouts and manually edit the bouts Rhythm selected or missed by either keeping selected bouts as is, extending the period to the observed start of recess, or deleting the selected bout. We normally observed a pattern in which a noticeable rise in temperature of an incubation bout was followed by some period of stability. Raven Pro plotted the ambient temperatures along with iButton incubation temperatures to more accurately determine when a female was on or off the nest. This data allowed us to calculate the number of incubation bouts per day, average incubation bout duration in minutes per day, and total minutes of incubation per day throughout the incubation period. This study was carried out in accordance with recommendations of the Institutional Animal Care and Use Committee of the University of Nevada, Reno.

Statistical Analysis

For statistical analyses, all models were run with R version 3.6.1 (R Core Team, 2019). Using the *lme4* package, we performed a generalized linear mixed-effects model (GLMM) using the glmer function and linear mixed models (LMM) using the lmer function. We used the *lmerTest* package to report all p-values. All final models met assumptions of normality and homoscedasticity of residual errors. Significance was taken at $\alpha = 0.05$. We used the cohen.d function in the *effsize* package to calculate all effect sizes. Females at the rural site started incubating at earlier Julian dates than urban females (coef = 0.1, s.e. = 0.05, z-value = 2.2, $p = 0.03$). Therefore, to avoid collinearity, we did not include Julian date in the models. We subsetted our data to include only data in which Julian dates overlapped at both sites and ensured that our reported results were consistent with this subset dataset.

For all models, we included the interaction of site and incubation day as a fixed effect and nest ID as a random effect. When the interaction was not significant, we removed the interaction term and tested the fixed effects independently. Including clutch size and egg mass was insignificant in all models and thus removed. In this study, neither clutch size nor egg mass differed between the urban and rural birds (clutch size: $t = 1.4$, df = 13.0, $p = 0.2$; egg mass: df = 21.7, $t = -0.8$, $p = 0.4$). Hatching success also did not differ between the urban and rural birds ($t = -0.9$, df = 12.2, $p = 0.4$). We used a GLMM with a Poisson distribution to test if the number of incubation bouts differed between the urban and rural site. A LMM was used to test the difference in average bout duration between the two sites. To meet linear model assumptions, we transformed average incubation duration, which was skewed to the right, by taking the reciprocal. We used a LMM to test if total daily incubation duration differed between the two sites. For this model, we removed two statistical outliers to ensure the statistical assumption of normality of residuals. We note that our results remain the same whether or not we include these outliers.

RESULTS

We had complete incubation recordings (11 days per nest) for eight urban and seven rural nests. Urban females had more incubation bouts per day than rural females (**Figure 1A** and **Table 1**) with a large effect size (Cohen's $D = -1.52$). Urban mothers had on average shorter incubation bouts than rural mothers (**Figure 1B** and **Table 1**) with a large effect size (Cohen's $D = -1.88$). There was a significant interaction between site and day for average incubation duration (**Table 1**). As the incubation period progressed, urban females decreased average bout duration while rural females' average bouts duration was maintained (**Figure 1B**). Additionally, rural females spent more total time incubating per day than urban females (**Figure 1C** and **Table 1**) with a large effect size (Cohen's $D = 1.51$). There was a significant interaction between site and day for the total incubation duration (**Table 1**). Rural females increased total incubation duration as incubation period progressed but urban females did not (**Figure 1C**).

DISCUSSION

We measured incubation behavior of urban and rural house wrens to determine whether differences in the urban environment influenced parental behavior during incubation. We found that urban females had more and shorter daily incubation bouts leading to less total time spent incubating eggs over the entire incubation period. However, our study is limited in its lack of site replicates. Therefore, while the results are promising, we caution the extrapolation of our results to other urban and rural areas that may differ in environmental pressures.

Urban house wren females had a higher number of incubation bouts per day (on average nine more bouts per day), meaning females were on and off the eggs more often compared to

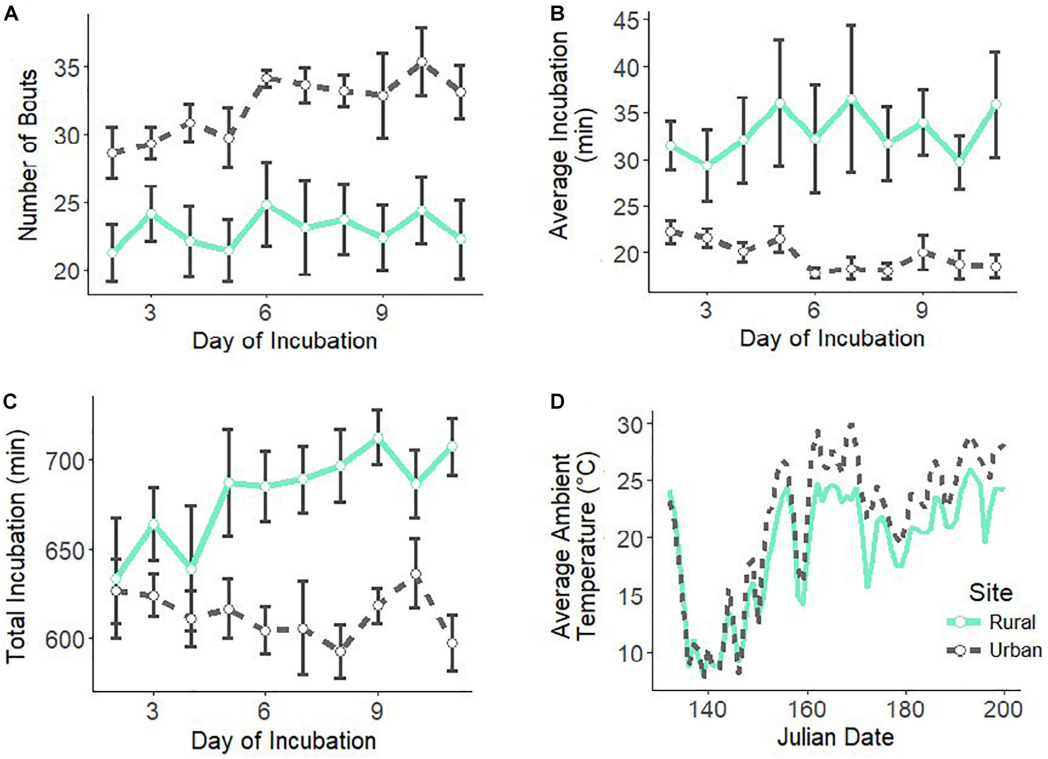

FIGURE 1 | Female house wren incubation behaviors over the 11 days of incubation, including number of incubation bouts **(A)**, average incubation bout duration **(B)**, and total incubation duration **(C)**. Ambient daytime temperatures are shown for both sites throughout the breeding season **(D)**. Urban site and females are in black, dotted lines and rural site and females are in green, solid lines. Shown are means ± 1 SE.

TABLE 1 | Results from generalized linear mixed model (number of incubation bouts) and linear mixed models (average and total incubation duration) analyzing differences in incubation behavior between urban and rural house wren females.

Incubation behavior	Coefficient	SE	*z*	*p*
Number of incubation bouts:				
Site	0.350	0.088	3.998	**0.000**
Day of Incubation	0.014	0.005	2.541	**0.011**
	Coefficient	**SE**	***t***	***p***
Average incubation duration:				
Site	0.010	0.005	2.235	**0.033**
Day of Incubation	<−0.001	<0.001	−0.567	0.572
Site: Day of Incubation	0.001	<0.001	3.105	**0.002**
Total incubation duration:				
Site	−36.144	21.333	−1.694	0.095
Day of Incubation	4.509	1.871	2.410	**0.017**
Site: Day of Incubation	−5.779	2.532	−2.283	**0.024**

Fixed effects that were significant ($p < 0.05$) are highlighted in bold. Nest ID was included as a random effect to correct for repeated sampling of individual females over different incubation days.

rural females. Incubation is an extremely energetically costly aspect of parental care (Vleck, 1981; Thomson et al., 1998; Tinbergen and Williams, 2002) in which parents must cope with varying environmental conditions and adjust the balance between incubation and self-maintenance (Conway and Martin, 2000b; Nord and Williams, 2015). Cities often experience higher disturbance from increase traffic noise (Mulholland et al., 2018), human disturbance (Markovchick-Nicholls et al., 2008), and new predator compositions (Rodewald and Kearns, 2011), which all may force females to leave the nest more often.

Each incubation bout was also shorter in duration for urban females by on average 13 min. The "energetic-bottleneck" hypothesis states that incubation effort is dependent on energy availability acquired through self-maintenance (Yom-Tov and Hilborn, 1981). Therefore, female's incubation effort can depend on a variety of factors including food availability, foraging efficiency, and amount of time allowed off the nest to forage. In species such as house wrens in which females incubate alone, but are provisioned by mates to some extent, incubation limits time for foraging (Skutch, 1962; Jones, 1987; Monaghan and Nager, 2002). Urban environments pose challenges of reduced nutritious food and limited food availability (Chamberlain et al., 2009), which is mirrored in this study (Baldan and Ouyang, 2020). If birds are faced with lower foraging efficiency and abundance of food in urban habitats, females may need to take shorter incubation bouts and longer foraging bouts to meet their own energetic demands (Conway and Martin, 2000b). Lack of predation risk can be another reason we see these differences (Thompson, 2007). While longer incubation and recess bouts would limit nest activity and decrease risk of predation (Conway and Martin, 2000b), urban birds may move on and off the nest more often with shorter bouts because they experience lower risk of predation in urbanized habitats (J Heppner per obs, Vincze et al., 2017; Eötvös et al., 2018).

As the number of shortened bouts increases, these behaviors in urban females all lead to a total shortened period of incubation by an average of 67 min. Temperature is one of the most critical aspects of successful incubation, and the urban heat island, a byproduct of urbanization in which cities have higher temperatures than surrounding natural lands, could have lasting effects. Our urban site had an average of 2.3°C higher temperatures than our rural site (**Figure 1D**). The majority of studies have reported that incubating adults respond to elevated temperatures by decreasing incubation effort due to reduced thermostatic demand (Kendeigh, 1952; Haftorn, 1979; Conway and Martin, 2000a,b; Londoño et al., 2008; Camfield and Martin, 2009; Álvarez and Barba, 2014; Amininasab et al., 2016). For example, urban pale breasted thrush (*Turdus leucomelas*) that built their nests on buildings decreased nest attentiveness as compared to ones that built nests on trees because buildings increase nest temperatures (Batisteli et al., 2020). In a recent laboratory experiment, elevated ambient temperatures decreased female incubation attentiveness in zebra finches (*Taeniopygia guttata*) (Ton et al., 2021). Therefore, elevated ambient temperatures in urban habitats may be one environmental pressure driving differences in incubation behavior of urban birds.

Incubating adults will adjust their incubation patterns to maximize fitness, for example when they are energetically constrained (Skutch, 1962; Deeming, 2002a). Thus, we propose two possible hypotheses as to the mechanisms driving the observed behavioral changes. The first is that urban females decrease nest attentiveness because increased ambient temperatures allow them the opportunity (reduced thermal costs). Experiencing higher ambient temperature in urban areas may allow females to compensate for reduced foraging efficiency by spending more time off the nest foraging for themselves (Conway and Martin, 2000a,b; Londoño et al., 2008). Higher temperatures in nest boxes overnight may reduce the thermostatic costs of incubating adults, allowing them to have higher energy stores (Bryan and Bryant, 1999), which may permit incubating adults to decrease nest attentiveness and increase time off the nest. Further studies investigating nighttime allocation of energy is warranted to disentangle the temporal distribution of female energetic expenditure during incubation. An alternative but non-mutually exclusive explanation is that urban birds decrease incubation effort because they are required to spend more time foraging due to lower availability of food to acquire the needed energy for incubation. This possibility could come at a cost to the offspring in terms of hatching success (Charmantier et al., 2017). However, we saw no difference in hatching success between our urban and rural nests, possibly suggesting a reduced cost of incubation for urban females. Egg and microclimate temperature within the nest would be needed to fully understand the effects of ambient temperature on these behaviors.

As the incubation period progressed, urban females spent less time on average incubating during a bout while this duration stayed relatively constant for rural females (**Figure 1B**). Additionally, while total incubation time in rural birds increased over the course of the period, urban females remained relatively constant (**Figure 1C**). Why would urban and rural birds differ in intensity of these behaviors as incubation day progresses? Temperate birds such as house wrens, normally display a rapid increase in nest attentiveness once the full clutch is laid and maintain this level as hatching approaches (Kendeigh, 1952; Skutch, 1962), which is observed in our rural females (**Figure 1C**). As food availability is lower at our urban site, it supports why urban females do not mirror the expected increase in incubation time of their rural counterparts and have a lower, yet consistent, incubation effort as more time may need to be spent foraging for food. More experimental studies are needed to disentangle the directionality and duration of these behavioral differences in urban and rural female incubation.

While there is growing evidence for behavioral adjustments in urban environments, it is difficult to conclude whether these shifts are caused by plasticity or evolutionary processes (Sol et al., 2013). Birds in particular are able to tolerate new conditions and environments due to behavioral, physiological and ecological flexibility (Bonier et al., 2007). The individuals that colonize urban environments may possess more behavioral plasticity in their incubation strategies (Haftorn, 1979; Sol et al., 2013; McClintock et al., 2014; Marzluff, 2017; Simmonds et al., 2017). Adjusting incubation behavior can help avian wildlife cope with novel environmental challenges, ensure an optimal thermal environment for the developing embryos, and allow birds to inhabit urbanized areas. As incubation temperature affects offspring fitness (Hepp et al., 2015; Ospina, 2017), behavioral alternations can also be a mechanism producing phenotypic differences in urban birds. Urban heat island effects, combined with previously described ambient temperature and predation effects (Conway and Martin, 2000b), may together drive selective forces in urban birds.

Urbanization poses a suite of new challenges which influence life-time fitness (Conway and Martin, 2000b; McDonnell and Hahs, 2015; Sepp et al., 2018). While urbanization has changed the biotic and abiotic environment, the characteristics that distinguish the persistence of urban wildlife are poorly understood (Bonier et al., 2007). Our study suggests that urbanization may be linked to an essential aspect of avian reproduction and parental care. However, our study is correlative, and experimental studies are needed to test whether this shift in behavior is due to plasticity or adaptation. Our study also only had one urban and one rural site; therefore, these results may not be representative of other urbanized landscapes. Due to this limitation, we caution from general interpretations and highly urge further studies across multiple urban to rural gradients to better understand the patterns between urbanization and behavioral shifts. However, this study gives an initial insight to altered behaviors due to environmental change. By studying trait differences between urban and non-urban wildlife, we can better understand urbanization's effects on wildlife behavior and how these parental behaviors affect offspring phenotypes in a changing landscape.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The animal study was reviewed and approved by the Institutional Animal Care and Use Committee of the University of Nevada, Reno.

AUTHOR CONTRIBUTIONS

JH and JO conceived the study. JO secured funding for the study. JH collected and analyzed the data and wrote the manuscript. Both authors revised, edited, and approved the manuscript before submission.

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REFERENCES

Álvarez, E., and Barba, E. (2014). Behavioural responses of great tits to experimental manipulation of nest temperature during incubation. *Ornis Fenn.* 91, 220–230.

Amininasab, S. M., Kingma, S. A., Birker, M., Hildenbrandt, H., and Komdeur, J. (2016). The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird. *Behav. Ecol. Sociobiol.* 70, 1591–1600. doi: 10.1007/s00265-016-2167-2

Ardia, D. R., Pérez, J. H., and Clotfelter, E. D. (2010). Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows. *Proc. R. Soc. B Biol. Sci.* 277, 1881–1888. doi: 10.1098/rspb.2009.2138

Arnfield, A. J. (2003). Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat island. *Int. J. Climatol.* 23, 1–26. doi: 10.1002/joc.859

Baldan, D., and Ouyang, J. Q. (2020). Urban resources limit pair coordination over offspring provisioning. *Sci. Rep.* 10:15888. doi: 10.1038/s41598-020-72951-2

Batisteli, A. F., de Souza, L. B., Santieff, I. Z., Gomes, G., Soares, T. P., Pini, M., et al. (2020). Buildings promote higher incubation temperatures and reduce nest attentiveness in a Neotropical thrush. *Ibis (Lond. 1859)* 163, 79–89. doi: 10.1111/ibi.12863

Bonier, F., Martin, P. R., and Wingfield, J. C. (2007). Urban birds have broader environmental tolerance. *Biol. Lett.* 3, 670–673. doi: 10.1098/rsbl.2007.0349

Bryan, S. M., and Bryant, D. M. (1999). Heating nest-boxes reveals an energetic constraint on incubation behaviour in great tits, Parus major. *Proc. R. Soc. B Biol. Sci.* 266, 157–162. doi: 10.1098/rspb.1999.0616

Camfield, A. F., and Martin, K. (2009). The influence of ambient temperature on horned lark incubation behaviour in an alpine environment. *Behaviour* 146, 1615–1633. doi: 10.1163/156853909X463335

Chamberlain, D. E., Cannon, A. R., Toms, M. P., Leech, D. I., Hatchwell, B. J., and Gaston, K. J. (2009). Avian productivity in urban landscapes: a review and meta-analysis. *Ibis (Lond. 1859).* 151, 1–18. doi: 10.1111/j.1474-919X.2008.00899.x

Charmantier, A., Demeyrier, V., Lambrechts, M., Perret, S., and Grégoire, A. (2017). Urbanization is associated with divergence in pace-of-life in great tits. *Front. Ecol. Evol.* 5:53. doi: 10.3389/fevo.2017.00053

Chen, G., Li, X., Liu, X., Chen, Y., Liang, X., Leng, J., et al. (2020). Global projections of future urban land expansion under shared socioeconomic pathways. *Nat. Commun.* 11:537. doi: 10.1038/s41467-020-14386-x

Clucas, B., and Marzluff, J. M. (2012). Attitudes and actions toward birds in Urban areas: human cultural differences influence bird behavior. *Auk* 129, 8–16. doi: 10.1525/auk.2011.11121

Conway, C. J., and Martin, T. E. (2000a). Effects of ambient temperature on avian incubation behavior. *Behav. Ecol.* 11, 178–188. doi: 10.1093/beheco/11.2.178

Conway, C. J., and Martin, T. E. (2000b). Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution (N. Y).* 54, 670–685. doi: 10.1111/j.0014-3820.2000.tb00068.x

Cooper, C. B., and Mills, H. (2005). New software for quantifying incubation behavior from time-series recordings. *J. F. Ornithol.* 76, 352–356. doi: 10.1648/0273-8570-76.4.352

Deeming, D. C. (2002a). *Avian Incubation: Behaviour, Environment, and Evolution*. Oxford: Oxford University Press.

Deeming, D. C. (2002b). "Behaviour patterns during incubation," in *Avian Incubation: Behaviour, Environment, and Evolution*, ed. D. C. Deeming (Oxford: Oxford University Press), 63–87.

Deeming, D. C. (2002c). "Importance and evolution of incubation in avian reproduction," in *Avian Incubation: Behaviour, Environment, and Evolution*, ed. D. C. Deeming (Oxford: Oxford University Press), 1–7. doi: 10.1093/acprof:oso/9780198718666.003.0001

Durant, S. E., Hopkins, W. A., Hepp, G. R., and Walters, J. R. (2013). Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biol. Rev.* 88, 499–509. doi: 10.1111/brv.12015

Eötvös, C. B., Magura, T., and Lövei, G. L. (2018). A meta-analysis indicates reduced predation pressure with increasing urbanization. *Landsc. Urban Plan.* 180, 54–59. doi: 10.1016/j.landurbplan.2018.08.010

Gorissen, L., Snoeijs, T., Van Duyse, E., and Eens, M. (2005). Heavy metal pollution affects dawn singing behaviour in a small passerine bird. *Oecologia* 145, 504–509. doi: 10.1007/s00442-005-0091-7

Haftorn, S. (1979). Incubation and Regulation of Egg Temperature in the Willow Tit Parus montanus. *Ornis Scand. (Scandinavian J. Ornithol.)* 10, 220–234. doi: 10.2307/3676066

Hall, J. M., and Warner, D. A. (2018). Thermal spikes from the urban heat island increase mortality and alter physiology of lizard embryos. *J. Exp. Biol.* 221:jeb181552. doi: 10.1242/jeb.181552

Hepp, G. R., Durant, S. E., and Hopkins, W. A. (2015). "Influences of incubation temperature on offspring phenotype and fitness in birds," in *Nests, Eggs, and*

Incubation, eds D. C. Deeming and S. J. Reynolds (Oxford: Oxford University Press), 171–178. doi: 10.1093/acprof:oso/9780198718666.003.0014

Johnson, M. T. J., and Munshi-South, J. (2017). Evolution of life in urban environments. *Science* 358:eaam8327. doi: 10.1126/science.aam8327

Jones, G. (1987). Time and energy constraints during incubation in free-living swallows (Hirundo rustica): an experimental study using precision electronic balances. *J. Anim. Ecol.* 56:229. doi: 10.2307/4812

Kendeigh, S. C. (1952). *Parental Care and its Evolution in Birds. Illinois Biological Monographs*. Urbana: The University of Illinois Press.

Landsberg, H. E. (1981). *The Urban Climate. urban Clim*. New York: Academic Press. doi: 10.1016/0304-4009(83)90022-0.

Londoño, G. A., Levey, D. J., and Robinson, S. K. (2008). Effects of temperature and food on incubation behaviour of the northern mockingbird, Mimus polyglottos. *Anim. Behav.* 76, 669–677. doi: 10.1016/j.anbehav.2008.05.002

Mainwaring, M. C. (2015). "Nest construction and incubation in a changing climate," in *Nests, Eggs, and Incubation*, eds D. C. Deeming and S. J. Reynolds (Oxford: Oxford University Press), 65–74. doi: 10.1093/acprof:oso/9780198718666.003.0006

Markovchick-Nicholls, L., Regan, H. M., Deutschman, D. H., Widyanata, A., Martin, B., Noreke, L., et al. (2008). Relationships between human disturbance and wildlife land use in urban habitat fragments. *Conserv. Biol.* 22, 99–109. doi: 10.1111/j.1523-1739.2007.00846.x

Martin, T. E., and Ghalambor, C. K. (1999). Males feeding females during incubation. I. Required by microclimate or constrained by nest predation? *Am. Nat.* 153, 131–139. doi: 10.1086/303153

Marzluff, J. M. (2017). A decadal review of urban ornithology and a prospectus for the future. *Ibis (Lond. 1859).* 159, 1–13. doi: 10.1111/ibi.12430

McClintock, M. E., Hepp, G. R., and Kennamer, R. A. (2014). Plasticity of incubation behaviors helps Wood Ducks (Aix sponsa) maintain an optimal thermal environment for developing embryos. *Auk* 131, 672–680. doi: 10.1642/auk-14-57.1

McDonnell, M. J., and Hahs, A. K. (2015). Adaptation and Adaptedness of organisms to urban environments. *Annu. Rev. Ecol. Evol. Syst.* 46, 261–280. doi: 10.1146/annurev-ecolsys-112414-054258

Mckinney, M. L. (2002). Urbanization, biodiversity, and conservation. *BioScience* 52, 883–890.

Mckinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* 127, 247–260. doi: 10.1016/j.biocon.2005.09.005

Merrill, L., Ospina, E. A., Santymire, R. M., and Benson, T. J. (2020). Egg incubation temperature affects development of innate immune function in nestling American Robins (Turdus migratorius). *Physiol. Biochem. Zool.* 93, 1–12. doi: 10.1086/705361

Monaghan, P., and Nager, R. G. (2002). Why don't birds lay more eggs? *Qual. Saf. Heal. Care* 11:6. doi: 10.1136/qhc.11.1.6

Mulholland, T. I., Ferraro, D. M., Boland, K. C., Ivey, K. N., Le, M. L., LaRiccia, C. A., et al. (2018). Effects of experimental anthropogenic noise exposure on the reproductive success of secondary cavity nesting birds. *Integr. Comp. Biol.* 58, 967–976. doi: 10.1093/icb/icy079

Nord, A., and Cooper, C. B. (2019). Night conditions affect morning incubation behaviour differently across a latitudinal gradient. *Int. J. Avian Sci.* 162, 827–835. doi: 10.1111/ibi.12804

Nord, A., and Nilsson, J. Å (2011). Incubation temperature affects growth and energy metabolism in blue tit nestlings. *Am. Nat.* 178, 639–651. doi: 10.1086/662172

Nord, A., and Williams, J. B. (2015). "The energetic costs of incubation," in *Nests, Eggs, and Incubation*, eds D. C. Deeming and J. S. Ronalds (Oxford: Oxford University Press).

Ospina, E. A. (2017). *Incubation Temperature Impacts Growth, Physiology and Survival in Nestlings of an Open-Cup Nesting Passerine*. M.S. Thesis, University of Illinois at Urbana, Urbana, IL.

Ouyang, J. Q., Baldan, D., Munguia, C., and Davies, S. (2019). Genetic inheritance and environment determine endocrine plasticity to urban living. *Proc. R. Soc. B Biol. Sci.* 286:20191215. doi: 10.1098/rspb.2019.1215

Ouyang, J. Q., Isaksson, C., Schmidt, C., Hutton, P., Bonier, F., and Dominoni, D. (2018). A new framework for urban ecology: an integration of proximate and ultimate responses to anthropogenic change. *Integr. Comp. Biol.* 58, 915–928. doi: 10.1093/icb/icy110

Peng, S., Piao, S., Ciais, P., Friedlingstein, P., Ottle, C., Bréon, F. M., et al. (2012). Surface urban heat island across 419 global big cities. *Environ. Sci. Technol.* 46, 696–703. doi: 10.1021/es2030438

Pérez, J. H., Ardia, D. R., Chad, E. K., and Clotfelter, E. D. (2008). Experimental heating reveals nest temperature affects nestling condition in tree swallows (Tachycineta bicolor). *Biol. Lett.* 4, 468–471. doi: 10.1098/rsbl.2008.0266

R Core Team (2019). R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing.

Reynolds, J. S., Ibáñez-Álamo, J. D., Sumasgutner, P., and Mainwaring, M. C. (2019). Urbanisation and nest building in birds: a review of threats and opportunities. *J. Ornithol.* 160, 841–860. doi: 10.1007/s10336-019-01657-8

Rodewald, A. D., and Kearns, L. J. (2011). Shifts in dominant nest predators along a rural-to-urban landscape gradient. *Condor* 113, 899–906. doi: 10.1525/cond.2011.100132

Sepp, T., McGraw, K. J., Kaasik, A., and Giraudeau, M. (2018). A review of urban impacts on avian life-history evolution: does city living lead to slower pace of life? *Glob. Chang. Biol.* 24, 1452–1469. doi: 10.1111/gcb.13969

Seress, G., Hammer, T., Bókony, V., Vincze, E., Preiszner, B., Pipoly, I., et al. (2018). Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. *Ecol. Appl.* 28, 1143–1156. doi: 10.1002/eap.1730

Seress, G., and Liker, A. (2015). Habitat urbanization and its effects on birds. *Acta Zool. Acad. Sci. Hungaricae* 61, 373–408. doi: 10.17109/AZH.61.4.373.2015

Seress, G., Lipovits, Á, Bókony, V., and Czúni, L. (2014). Quantifying the urban gradient: a practical method for broad measurements. *Landsc. Urban Plan* 131, 42–50. doi: 10.1016/j.landurbplan.2014.07.010

Seress, G., Sándor, K., Evans, K. L., and Liker, A. (2020). Food availability limits avian reproduction in the city: an experimental study on great tits Parus major. *J. Anim. Ecol.* 89, 1570–1580. doi: 10.1111/1365-2656.13211

Shochat, E., Lerman, S., and Fernández-Juricic, E. (2010). "Birds in urban ecosystems: population dynamics, community structure, biodiversity, and conservation," in *Urban Ecosystem Ecology*, eds J. Aitkenhead-Peterson and A. Volder (Madison: ASA-CSSA-SSSA), 75–86. doi: 10.2134/agronmonogr55.c4

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., and Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.* 21, 186–191. doi: 10.1016/j.tree.2005.11.019

Sih, A., Ferrari, M. C. O., and Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* 4, 367–387. doi: 10.1111/j.1752-4571.2010.00166.x

Simmonds, E. G., Sheldon, B. C., Coulson, T., and Cole, E. F. (2017). Incubation behavior adjustments, driven by ambient temperature variation, improve synchrony between hatch dates and caterpillar peak in a wild bird population. *Ecol. Evol.* 7, 9415–9425. doi: 10.1002/ece3.3446

Skutch, A. F. (1962). The constancy of incubation. *Wilson Bull.* 74, 115–152. doi: 10.2307/4159040

Sol, D., Lapiedra, O., and González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Anim. Behav.* 85, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Thompson, F. R. (2007). Factors affecting nest predation on forest songbirds in North America. *Ibis (Lond. 1859).* 149, 98–109. doi: 10.1111/j.1474-919X.2007.00697.x

Thomson, D. L., Monaghan, P., and Furness, R. W. (1998). The demands of incubation and avian clutch size. *Biol. Rev.* 73, 293–304. doi: 10.1111/j.1469-185X.1998.tb00032.x

Tinbergen, J. M., and Williams, J. B. (2002). "Energetics of incubation," in *Avian Incubation: Behaviour, Environment, and Evolution*, ed. D. C. Deeming (Oxford: Oxford University Press), 299–313.

Ton, R., Hurley, L. L., and Griffith, S. C. (2021). Higher experimental ambient temperature decreases female incubation attentiveness in Zebra Finches (Taeniopygia guttata) and lower effort yields negligible energy savings. *Int. J. Avian Sci.* doi: 10.1111/ibi.12922

United Nations (2018). *World Urbanization Prospects. Department of Economic and Social Affairs, Population Division*. New York, NY: United Nations.

Vincze, E., Seress, G., Lagisz, M., Nakagawa, S., Dingemanse, N. J., and Sprau, P. (2017). Does urbanization affect predation of bird nests? A meta-analysis. *Front. Ecol. Evol.* 5:29. doi: 10.3389/fevo.2017.00029

Vleck, C. M. (1981). Energetic cost of incubation in the zebra finch. *Con* 83, 229–237. doi: 10.2307/1367313

Yom-Tov, Y., and Hilborn, R. (1981). Energetic constraints on clutch size and time of breeding in temperate zone birds. *Oecologia* 48, 234–243. doi: 10.1007/BF00347969

Zhang, W. W., and Ma, J. Z. (2011). Waterbirds as bioindicators of wetland heavy metal pollution. *Procedia Environ. Sci.* 10, 2769–2774. doi: 10.1016/j.proenv.2011.09.429

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Noise-Related Song Variation Affects Communication: Bananaquits Adjust Vocally to Playback of Elaborate or Simple Songs

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Birds communicate through acoustic variation in their songs for territorial defense and mate attraction. Noisy urban conditions often induce vocal changes that can alleviate masking problems, but that may also affect signal value. We investigated this potential for a functional compromise in a neotropical songbird: the bananaquit (*Coereba flaveola*). This species occurs in urban environments with variable traffic noise levels and was previously found to reduce song elaboration in concert with a noise-dependent reduction in song frequency bandwidth. Singing higher and in a narrower bandwidth may make their songs more audible in noisy conditions of low-frequency traffic. However, it was unknown whether the associated decrease in syllable diversity affected their communication. Here we show that bananaquits responded differently to experimental playback of elaborate vs. simple songs. The variation in syllable diversity did not affect general response strength, but the tested birds gave acoustically distinct song replies. Songs had fewer syllables and were lower in frequency and of wider bandwidth when individuals responded to elaborate songs compared to simple songs. This result suggests that noise-dependent vocal restrictions may change the signal value of songs and compromise their communicative function. It remains to be investigated whether there are consequences for individual fitness and how such effects may alter the diversity and density of the avian community in noisy cities.

Keywords: song elaboration, song complexity, signal quality, territoriality, syllable repertoire

INTRODUCTION

In the last decades, the noise levels in human-altered and natural habitats have substantially increased and affected the way birds sing (Rabin and Greene, 2002; Mennitt et al., 2015; Buxton et al., 2017). Anthropogenic noise can interfere with communication among birds because it can mask their songs through overlap in frequency and time (Brumm and Slabbekoorn, 2005; Barber et al., 2010; Parris and McCarthy, 2013). Several noise-dependent vocal changes have been reported in city birds (Brumm, 2004; Potvin and Mulder, 2013; Gil et al., 2014), which typically yield an increase in song detectability and improved efficiency of communication (Brumm and Slabbekoorn, 2005; Pohl et al., 2012). However, vocal changes may not only affect signal detectability but also signal value (Slabbekoorn and Ripmeester, 2008; Gross et al., 2010) and noise-dependent song variation may thereby involve a functional compromise (Slabbekoorn, 2013; Luther and Magnotti, 2014; Luther et al., 2016; Phillips and Derryberry, 2018). Although reports on noise-dependent song variation are widespread, tests of the potential for functional consequences for communication are still rare (see e.g., Mockford and Marshall, 2009; Ripmeester et al., 2010; Luther and Derryberry, 2012; Luther et al., 2016).

There are several ways birds change their songs by which they could counteract masking by urban noise. Several species have been found to sing higher frequencies and/or narrower-banded songs in noisier environments (Slabbekoorn and Peet, 2003; Verzijden et al., 2010; Bermúdez-Cuamatzin et al., 2011; Montague et al., 2012; LaZerte et al., 2016). As anthropogenic noise is typically biased to low-frequency bands, higher-frequency songs are more audible than lower-frequency songs (Brumm and Slabbekoorn, 2005; Nemeth and Brumm, 2010; Halfwerk et al., 2011) and concentrating all acoustic energy in a narrower band can also raise signal-to-noise ratio (Hanna et al., 2011). Birds are also reported to sing at higher amplitudes if noise levels rise and they can sing shorter or in alternating time periods when noise levels are fluctuating (Brumm, 2004; Gil et al., 2014; Gentry et al., 2017; Derryberry et al., 2017).

Although such noise-dependent changes may be successful in masking avoidance, they may also restrict the potential for communication by undermining the signaling function of the songs (Slabbekoorn and Ripmeester, 2008; Gross et al., 2010; Slabbekoorn, 2013; Luther et al., 2016). Reduction in frequency band use, for example, may restrict the use of particular syllables and limit possible syllable variation, and consequently limit song repertoire size of an individual (Montague et al., 2012; Fouda et al., 2018; Winandy et al., 2021). Song elaboration in birds may signal male size or other parental qualities (e.g., Kipper et al., 2006; Botero et al., 2009; Kagawa and Soma, 2013) and can be a good predictor of potential offspring survival and thus affect female preference (Hasselquist et al., 1996; Buchanan and Catchpole, 1997, 2000). Although, some bird species may be able to counteract song structure restrictions on song complexity (see Moseley et al., 2019), noise-dependent reduction in song elaboration in general may negatively affect signal quality and undermine information transfer about sender quality.

Potential signal value or communicative function of a song can be explored by controlled exposure to playbacks of recorded songs and by experimental manipulation of specific acoustic variation (e.g., Nelson, 1988; Slabbekoorn and ten Cate, 1998; Linhart et al., 2012). Playback of urban and rural song variation has, for example, revealed recognition of urban acoustic features in natural territories of great tits (*Parus major*) and European blackbirds (*Turdus merula*). Individual birds approach more closely, stay longer or respond vocally more quickly to playback of songs dependent on whether they are from birds from the same habitat type or similar background noise levels (Mockford and Marshall, 2009; Ripmeester et al., 2010). The potential impact of noise-dependent variation in spectral range has been tested in few studies in both male-female (Halfwerk et al., 2011; Huet des Aunay et al., 2014) and male-male communication (Luther and Magnotti, 2014; Luther et al., 2016; LaZerte et al., 2017; Phillips and Derryberry, 2018).

The bananaquit (*Coereba flavoela*), an abundant bird species of neotropical cities, is a good system to study the potential signal value of song elaboration. We previously showed bananaquits exhibit noise-dependent variation in song elaboration: they sing elaborate songs, rich in syllable types and syllable transitions in quiet territories and simple and repetitive songs that are poor in syllable diversity in more noisy territories (Winandy et al., 2021). They are relatively abundant across city habitats, used to human presence, and can be highly territorial to conspecific intruders (Hilty and Christie, 2018; personal observations). Consequently, bananaquits are very suitable for playback studies that demand close approach of researchers for behavioral observations and recordings.

In this study, we performed a playback exposure experiment and tested whether bananaquits responded differently to elaborate vs. simple songs. More elaborate songs were characterized by higher syllable diversity (i.e., more syllable types per song), but also by lower minimum and higher maximum frequencies (Winandy et al., 2021). In many species of birds, songs with an aggressive territorial function tend to be shorter and more repetitive than songs with a mate attraction function (Searcy and Anderson, 1986; Collins, 2004). Bananaquit territorial responses to playback may therefore be stronger to simpler songs and may also elicit a vocal response matching in song elaboration. More elaborate songs may require a wider frequency bandwidth. Consequently, we aimed at answering the following questions: (1) do simpler songs trigger stronger responses than the more elaborate songs? (2) do individuals match song elaboration? (3) do elaborate songs trigger wider frequency range songs from territory owners? This study could provide new insights into how noise pollution, through the simplification of urban songs, can alter the evolution of sexually selected signals.

MATERIALS AND METHODS

Ethics

The animal study was reviewed and approved by the local "Committee of Ethics in the Use of Animals," Federal University of Bahia – UFBA, Brazil (n°36/2016).

Study Site and Species

We conducted our playback experiment in 20 bananaquit (*Coereba flaveola*) territories in the city of Salvador, Bahia, Brazil (12°57′50.9″S, 38°′30′21.0″W). We tested the birds during the Brazilian summer, between February and March of 2018. This species can sing and breed throughout the year (Hilty and Christie, 2018) and territorial responsiveness does not fade during summer. The territories were located in different habitat types and traffic noise regimes: in Atlantic Forest urban parks, urban gardens and areas close or next to main avenues, with variable stands of concrete buildings and trees. We performed the experiment only during relatively quiet moments of the day for each territory, between 05H00 and 07H00 in the morning. Previous to the experiment, we assessed the noise levels of the territories throughout the morning, i.e., 05H00 to 10H00, with a sound pressure level meter, and the results are reported in Winandy et al. (2021). Noise levels rose gradually to become above 55dB(A) only after 07H00. By conducting our experiments before 07H00, before the rush hour, and by keeping the distance between playback speaker and response bird less than 14 m, we avoided possible interference of traffic noise with playback song detection, which was not our target in this study.

Bananaquits are nectarivorous songbirds that occur across the Neotropics from Mexico to Argentina and the Caribbean islands. They can be easily observed in several types of human-altered habitats, from highly urban to rural areas. They are territorial birds that sing for mate attraction and territorial defense throughout the day and year (Hilty and Christie, 2018). The singing is thought to be primarily done by males, although more research is needed about possible singing behavior in females (Riebel et al., 2019). The songs are composed of series of high-pitched syllables, which vary from complex sequences of diverse element types with high transition rates to highly repetitive series of less variable syllable types (Winandy et al., 2021). Bananquits have highly variable repertoires, and song elaboration may vary within and among individuals with behavioral context and local noise levels (Winandy et al., 2021).

Sound Recording and Analysis

Before exposing the birds to the playback, we recorded their pre-playback songs for 1 min. Usually, in 1 min of recording the bananaquits sang about 10 songs, but for some individuals we obtained less than five songs. We recorded the birds from a distance of 2–14 m, using a Tascam DR-44WL recorder connected to a Sennheiser TM (Wedemark, Germany) shotgun directional microphone (ME67 + K6). In total, we performed acoustic analyses on 11.1 ± 5.2 (mean ± SD) songs per individual. We used Raven TM PRO software, version 1.5 (Cornell Laboratory of Ornithology, Ithaca, NY, United States) for all processing of recordings and song measurements. Spectrograms settings were kept constant as: FFT length: 512, window: hann, overlap: 75%.

All song recordings, pre-playback and response songs, were first cut in shorter song sequences, separated from recorded playback stimuli, before the analyses. In this way, the observer was always blind to the origin and nature of songs in the stimuli used for the playback experiment. We used cursor placement to extract three spectral song variables (c.f. Verzijden et al., 2010; Winandy et al., 2021): minimum frequency, maximum frequency, and frequency bandwidth. The low-noise conditions during playback and the observer being blind to the stimulus type reduced the chance for observer bias or artifact effects in our spectral measurements (Verzijden et al., 2010; Brumm et al., 2017). Additionally, we counted the number of syllable types per song as a measure of song elaboration.

Playback Stimuli

We used songs of 20 bananaquits recorded at our study site in 2016 and 2017. We chose 20 song recordings varying in levels of song elaboration, from 10 individuals that sang relatively elaborate and from 10 individuals that sang relatively simple songs. Song elaboration is reflected in the number of different syllable types per song (MEAN ± SD simple = 3.1 ± 0.77, MEAN ± SD elaborate = 5.7 ± 1.6, Poisson GLM: Estimate = −0.618, N = 20, $P < 0.05$, **Figure 1**) and in the minimum and maximum song frequencies [two-way ANOVA for minimum frequency: MEAN ± SD simple = 3935.7 ± 516.5, MEAN ± SD elaborate = 2441.6 ± 590.8, $F(1, 19) = 35.55$, $N = 20$, $P < 0.001$, maximum frequency: MEAN ± SD simple = 12675.4 ± 494.4, MEAN ± SD elaborate = 11938.0 ± 840.4, $F(1, 19) = 6.14$, $N = 20$, $P = 0.02$, **Figure 1**]. We made sure that there were no significant differences in the length (measured in total number of syllables per song and song duration), peak frequency, syllable rate and frequency bandwidth between the two song categories [Poisson GLM for number of syllables: Estimate = 0.0366, $N = 20$, $P = 0.7$, song duration: $F(1, 19) = 3.37$, $N = 20$, $P = 0.08$, peak frequency: $F(1, 19) = 1.21$, $P = 0.2$, $N = 20$, syllable rate: $F(1, 19) = 2.444$, $N = 20$, $P = 0.135$, frequency bandwidth: $F(1, 19) = 2.928$, $N = 20$, $P = 0.1$], as they may also convey information and, for example, be indicative for motivational states of birds (Langemann et al., 2000; Ripmeester et al., 2007; Lattin and Ritchison, 2009; Linhart et al., 2012, 2013; Luther et al., 2016; Phillips and Derryberry, 2017). All the songs were high-pass filtered to remove the low-frequency background noise and normalized to an equal peak amplitude in Audacity TM v. 2.1.2 (Carnegie Mellon University, Pittsburgh, Pennsylvania, United States).

Each playback stimulus consisted of three different songs of the same individual and song category (simple or elaborate). Songs from the same individual were only used for one stimulus and thus not in different song categories. The three songs were played back twice in the same sequence with a silent interval of 3 s between each of them (c.f. Ripmeester et al., 2010). We created in this way 10 unique exemplars of each playback stimulus: 10 simple and 10 elaborate playback stimuli.

Playback Design

We played back the stimulus songs in bananaquit territories of actively singing birds without nearby competitors that could be agonistically interacting at the time of the experiment. These procedures were meant to reduce variation in behavioral responses related to different motivational states. We placed the ‘JBL clip 2’ loudspeaker at about 5–10 m from the focal male and the observer was positioned 5–10 m further away. We measured the amplitude of the playback with a Skill-Tec TM, SKDEC-02 (São Paulo, São Paulo, Brazil) sound pressure level meter (A-weighted, fast response, range 30–130 dB, 1 s interval) and adjusted playback levels to a volume of 70 dB(A) at a distance of 1 m from the speaker. After the start of the playback of the first song stimulus series, simple or elaborate, we scored the behavior of the focal individual for 1 min. During the playback and for 2 min after it had ended, we also recorded the songs. After the 2 min interval, we played back a song stimulus from the opposite

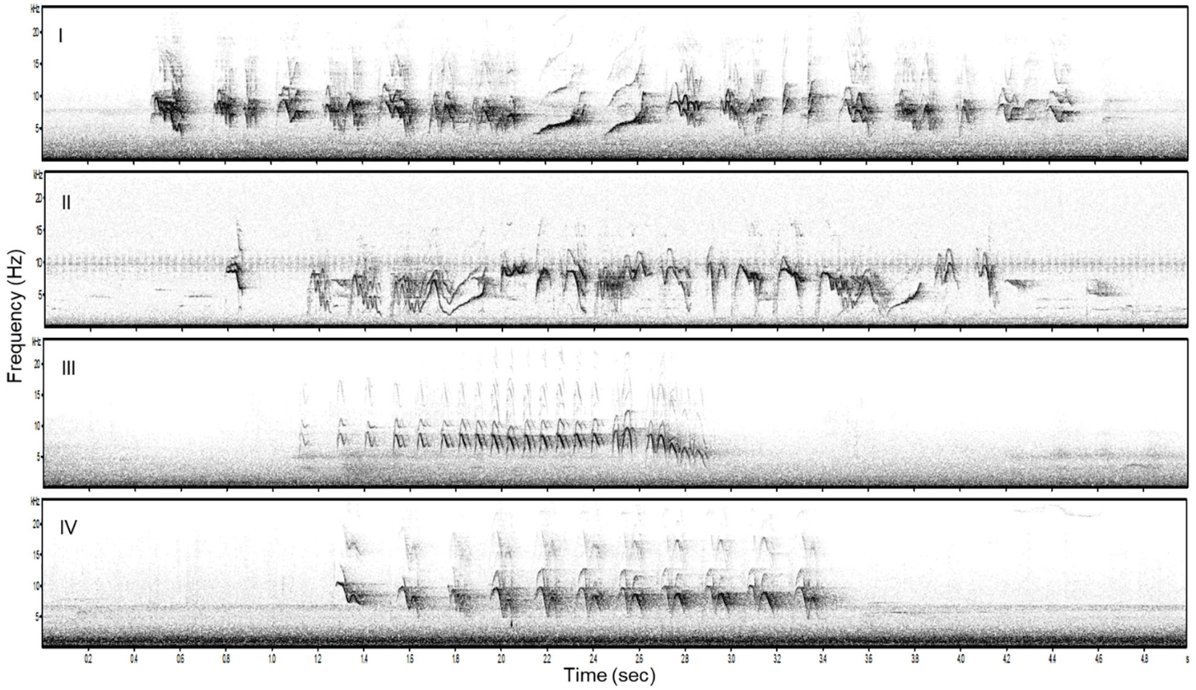

FIGURE 1 | Examples of two elaborate (I and II) and two simple (III, IV) song stimuli used in the playback experiment.

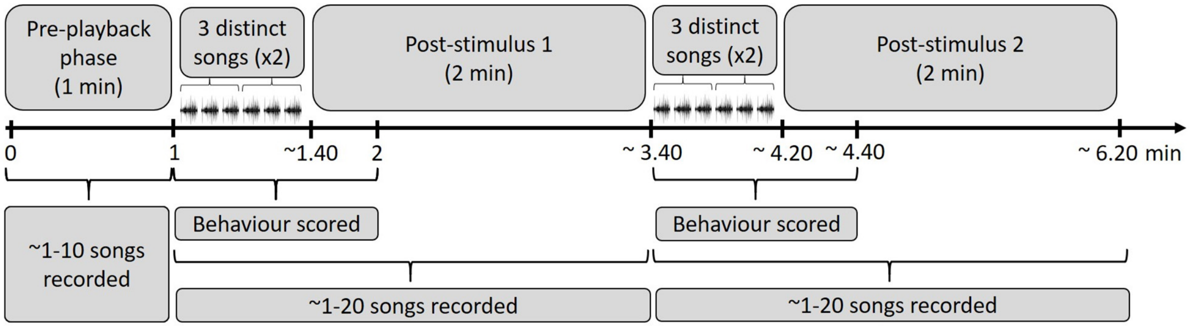

FIGURE 2 | Time periods overview of the playback procedure in the field. A stimulus of three distinct elaborate or simple songs of the same individual was played twice after a 1 min of pre-playback recording phase. After the start of the playback of the first song stimulus series, we scored behavior for 1 min. During the playback and for 2 min after it ended, we recorded the response songs. Following that, the second stimulus was played back to the same focal individual: three distinct songs twice of the opposite stimulus category (simple or elaborate songs, depending on the order of exposure).

category and recorded songs and scored response behaviors for the same periods as before (**Figure 2**). The order of the played back stimuli was randomized. We avoided testing direct neighbors that could have been exposed to previous playbacks. The following behaviors and song measurements were scored: number of flights over the loudspeaker, shortest distance of the focal male to the loudspeaker, number of songs, number of calls and song and call rate.

Statistical Analysis

We conducted all statistical analyses in R studio software (R Core Team), using the packages lme4 (Bates et al., 2015) and MuMIn (Barton, 2016). We performed generalized linear models (GLM) and Akaike's information criterion (AIC) model selection to find out whether the song variables and behavioral responses were affected by the stimulus type (simple vs. elaborate song playbacks) and/or by the order of the stimuli. All song measurements and behavioral responses were entered as response variables in the models. The stimulus category and playback order were entered as fixed factors in the full model and individual as random factor. We computed the statistics for all possible models, which included: (1) single predictors (stimulus category, order), (2) their additive combinations (category + order), and (3) the null models (without effect of any predictor). The response variables: number of syllable types, total number of syllables and number of flights were entered as interval variables in Poisson generalized models with log-link function.

We selected the best models based on the AICc values, considering ΔAICc > 2 a criterion for substantial difference between models (Burnham and Anderson, 2002). The model selection was made using the function dredge model selection (package MuMIn) (Barton, 2016). We calculated the marginal (R^2m) and conditional (R^2c) R^2 values to evaluate how much the fixed effects (R^2m) or the entire model (R^2c) explained the variance of the response variables (Nakagawa and Schielzeth, 2013). Finally, we performed *post-hoc* Tukey's tests for each response variable for which we obtained a minimal model selection. This analysis informed which pairs of playback conditions were significantly different in song or behavioral responses.

As we did in our previous correlational study, we investigated again the possible trade-off between the signal frequency reduction and the restriction in song elaboration. Therefore, we fitted linear models to test the relationship between the spectral and elaboration variables with two different datasets: one that included only the spontaneous songs sung before the start of the playback experiment and another with all songs, both the spontaneous and playback triggered songs.

RESULTS

There was no effect of the stimulus type (elaborate vs. simple) on behavioral response strength and vocalization rate. The number of flights, the approach to the speaker, the song and call rates were all not affected by stimulus category or by the playback order (**Table 1** and **Figure 3**). However, individuals responded in acoustically distinct ways to each playback type. Their songs had fewer syllables and were lower in frequency and wider in frequency bandwidth when they responded to the elaborate song stimuli compared to when they responded to the simple song stimuli (**Figure 4**).

The model selection for song variables showed that the number of syllables per song was significantly affected by the playback stimulus (**Table 2**). The birds sang fewer syllables per song after being exposed to the elaborate song stimulus than before the playback experiment, 12.42 syllables on average before and 11.40 on average after the elaborate playback stimulus (**Table 3**). The spectral variables: minimum frequency, maximum frequency and frequency bandwidth (Hz) were explained by both the song stimulus category and the order of the stimulus playback (**Table 2**). Regarding the order, when the elaborate stimulus was played first, the differences in the spectral responses between treatments were more pronounced (**Figure 4**). Birds significantly lowered the minimum frequency of their songs after being exposed to the elaborate playback (**Figure 4** and **Table 3**). Moreover, they sang songs of significantly wider frequency bandwidth when responding to the elaborate stimulus, followed by a bandwidth decrease when exposed to the simple playback as the second stimulus (**Figure 4** and **Table 3**).

Finally, the correlation between song elaboration and song frequency previously found for bananaquit songs was not found for the songs from the playback experiment in the current study. The number of syllable types per song and the spectral variables, minimum song frequency and frequency bandwidth, were not correlated. The correlation did not occur when we only included the spontaneous songs from the pre-playback phase [Linear model for low frequency: $R^2 = -0.06$, $F(1, 16) = 0.01$, $N = 17$, $P = 0.89$; Linear model for frequency bandwidth: $R^2 = -0.06$, $F(1, 16) = 0.03$, $N = 17$, $P = 0.86$] or when all songs from the playback experiment were included, i.e., for both spontaneous and playback triggered songs [Linear model for low frequency: $R^2 = -0.01$, $F(1, 53) = 0.05$, $N = 20$, $P = 0.81$; Linear model for frequency bandwidth: $R^2 = -0.01$, $F(1, 53) = 0.36$, $N = 20$, $P = 0.54$].

DISCUSSION

We performed a playback exposure experiment to test whether bananaquits responded differently to elaborate vs. simple songs. We found the following answers to our questions: (1) playback of simpler songs did not trigger stronger (or weaker) behavioral responses than playback of more elaborate songs; (2) individuals did not match song elaboration to the stimulus categories, and even decreased syllable numbers in their song in response to more elaborate songs; however (3) songs triggered by elaborate song playback had a lower minimum frequency and wider frequency range compared to songs sung before the playback. The frequency bandwidth of songs sung after the elaborate song playback were also significantly wider than songs sung after simple song playback.

Song Elaboration Is Meaningful

Our current results reveal that noise-induced changes in song elaboration concern meaningful changes to territorial birds in neotropical bananaquits. Variation in responsiveness related to variation in song elaboration is in line with other studies in the literature. In simulated territorial intrusions, for example, dark-eyed juncos (*Junco hyemalis*) responded stronger to structurally more elaborate songs, spending longer periods closer to the playback speaker (Reichard et al., 2011). In chaffinches (*Fringilla coelebs*), both males and females responded stronger to more elaborate songs, i.e., signals with a higher number of different trill phrases (Leitão et al., 2006), suggesting this song parameter plays a role in both male-male competition and mate attraction. As we found an impact of song elaboration on response song variation and not on response strength, a signaling function of this song feature may be widespread but vary in content among species.

The impact of song elaboration on response song variation in our study on bananaquits concerned syllable number and spectral variation. We found no matching in elaboration, as more elaborate stimuli led to less elaborate response songs. We did not expect this, as less elaborate and more stereotypic songs can be associated with male-male interactions, while more elaborate and diverse songs can be more important for female choice (Hasselquist et al., 1996; Searcy and Beecher, 2009; Kagawa and Soma, 2013). However, we did find spectral matching in the minimum song frequency and in an increase in the frequency

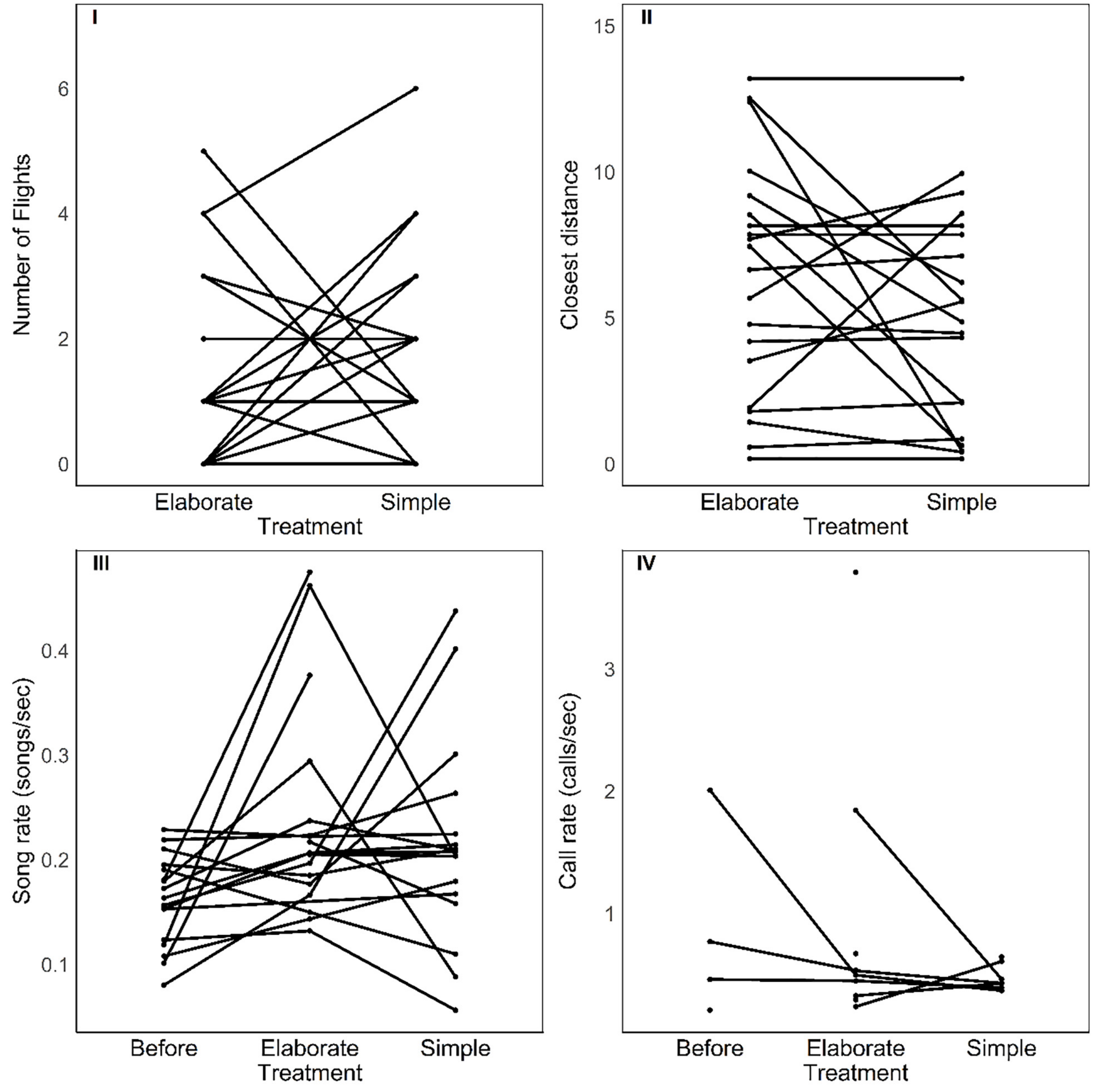

FIGURE 3 | Strength of behavioral responses to each song playback **(top)** and vocalization rate **(bottom)** before and during each song playback. There were no significant changes between scoring periods (see text).

bandwidth when individuals responded to the elaborate playback. Similar changes in song frequency use have been found to be meaningful in other species in various ways. Frequency song matching, for example, can be an aggressive signal between rival birds during dispute (Searcy and Beecher, 2009) as reported for Kentucky warblers (*Oporornis formosus*, Morton and Young, 1986) and black-capped chickadees (*Poecile atricapillus*, Horn et al., 1992; Otter et al., 2002). Relative frequency variation among communicating birds (i.e., frequency mismatch) may be important, as shown for willow warblers (*Phylloscopus trochilus*, Linhart and Fuchs, 2015). Wider frequency bandwidths can also indicate higher aggressiveness, as white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) respond less strongly to songs of restricted bandwidth (Luther et al., 2016; Phillips and Derryberry, 2018). Although we still have limited insight into the content of the message, we suggest that, according to the literature, the spectral variation and matching in bananaquit songs may also be meaningful.

The modified spectral response, in the absence of a strength in other behavioral responses, could also reflect that song elaboration plays a role in moderating territorial disputes (Slabbekoorn and ten Cate, 1996; Searcy and Nowicki, 2000;

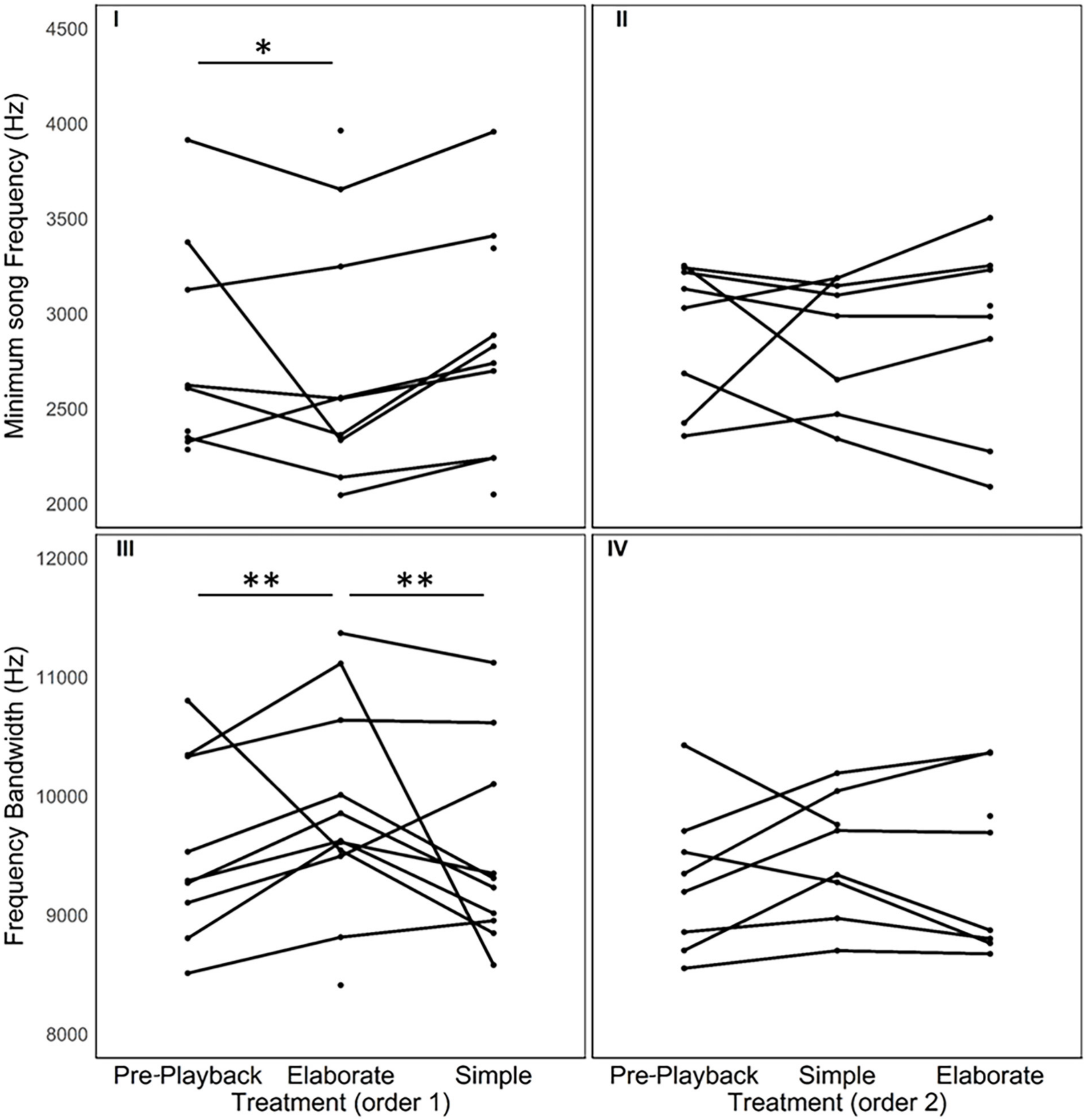

FIGURE 4 | Spectral variation in the songs sung in response to each stimulus category. Each line connects song measures of one individual in three different periods of the playback procedure. As playback order had an effect, we provide the data in two separate sets of graphs. Individuals that were exposed first to the elaborate songs followed by the simple songs are depicted in the graphs on the left. The responses of individuals that were exposed first to the simple songs followed by the elaborate songs are depicted in the graphs on the right. * indicates statistically significant differences between the measures in two of the playback periods ($*P < 0.05$ and $**P < 0.01$).

Otter et al., 2002). Graded variation in agonistic signals can convey increasing and decreasing levels of threats, before this becomes actually apparent in more overt changes in behavioral displays or approach tendencies (Searcy and Beecher, 2009). The fact that the order in which the stimuli were played influenced the escalation behavior of bananaquits in our study confirms such a possibility and warrants further exploration through playback experiments simulating dynamic changes in song elaboration (c.f. Hof and Podos, 2013).

Elaboration vs. Bandwidth as a Signal

There was an interesting discrepancy between the correlational analyses of the spectral and elaboration parameters in our previous (Winandy et al., 2021) and the current study. In the previous observational study, we found frequency bandwidth and

TABLE 1 | Results of the model selection for all behavioral response variables.

Model		Df	logLik	AICc	ΔAICc	weight	R^2m	R^2c
Number of flights ~ . . .								
1*	1 + (1| ID)	2	−70.4	145.1	0	0.38	0	0.08
2	Order + (1| ID)	3	−69.3	145.3	0.15	0.35	0.04	0.16
3	Playback + (1| ID)	3	−70.12	146.9	1.8	0.15	0.01	0.1
4	Playback + Order + (1| ID)	4	−69.13	147.4	2.28	0.12	0.05	0.16
Closest distance ~ . . .								
1*	1 + (1| ID)	3	−109.28	225.2	0	0.41	0	0.35
2	Playback + (1| ID)	4	−108.37	225.9	0.65	0.29	0.03	0.41
3	Order + (1| ID)	4	−108.88	226.9	1.67	0.18	0.01	0.38
4	Playback + Order + (1| ID)	5	−107.93	227.6	2.39	0.12	0.04	0.44
Song rate ~ . . .								
1*	Order + (1| ID)	4	53.99	−99.4	0	0.34	0.04	0.04
2	Playback + (1| ID)	5	55.1	−99.3	0.11	0.32	0.07	0.07
3	1 + (1| ID)	3	52.54	−98.7	0.66	0.24	0	0
4	Playback + Order + (1| ID)	6	55.1	−96.9	2.49	0.1	0.07	0.07
Call rate ~ . . .								
1*	1 + (1| ID)	3	−54.52	115.5	0	0.38	0	0.74
2	Playback + (1| ID)	5	−52.42	116.1	0.58	0.29	0.03	0.77
3	Playback + Order + (1| ID)	6	−51.48	116.7	1.23	0.21	0.03	0.79
4	Order + (1| ID)	4	−54.46	117.7	2.23	0.13	0	0.74

*ΔAICc > 2 indicates a significant difference between two models. R^2m indicates the proportion of variance of the response variable explained by the fixed factor and R^2c indicates the proportion of variance explained by the entire model. The bold values indicate the dependent variables of each model. *Indicates the best model. N = 20 individuals.*

TABLE 2 | Results of the model selection for all song response variables.

Model		df	logLik	AICc	ΔAICc	weight	R^2m	R^2c
Number of syllable types ~ . . .								
1*	1 + (1| ID)	2	−795.41	1594.9	0	0.45	0	0.08
2	Playback + (1| ID)	4	−793.89	1595.9	1.02	0.27	0.01	0.08
3	Order + (1| ID)	3	−795.34	1596.7	1.88	0.18	0	0.08
4	Playback + Order + (1| ID)	5	−793.88	1597.9	3.05	0.1	0.01	0.08
Number of syllables ~ . . .								
1*	Playback + (1| ID)	4	−1186.91	2381.9	0	0.57	0.01	0.28
2	Playback + Order + (1| ID)	5	−1186.5	2383.1	1.22	0.31	0.01	0.28
3	1 + (1| ID)	2	−1190.89	2385.8	3.89	0.08	0	0.28
4	Order + (1| ID)	3	−1190.65	2387.3	5.43	0.04	0	0.28
Minimum song frequency ~ . . .								
1*	Playback + Order + (1| ID)	6	−3243.93	6500.1	0	0.58	0.01	0.63
2	Playback + (1| ID)	5	−3245.51	6501.2	1.1	0.33	0.01	0.63
3	1 + (1| ID)	3	−3249.14	6504.3	4.28	0.07	0	0.62
4	Order + (1| ID)	4	−3249.06	6506.2	6.15	0.03	0	0.62
Maximum song frequency ~ . . .								
1*	Playback + Order + (1| ID)	6	−3352.68	6717.6	0	0.58	0.01	0.47
2	Playback + (1| ID)	5	−3354.86	6719.9	2.3	0.18	0.01	0.46
3	Order + (1| ID)	4	−3356.32	6720.7	3.18	0.12	0	0.46
4	1 + (1| ID)	3	−3357.34	6720.7	3.19	0.12	0	0.45
Frequency bandwidth ~ . . .								
1*	Playback + Order + (1| ID)	6	−3443.05	6898.3	0	0.95	0.02	0.56
2	Playback + (1| ID)	5	−3447.13	6904.4	6.11	0.05	0.01	0.56
3	Order + (1| ID)	4	−3451.92	6911.9	13.64	0	0	0.55
4	1 + (1| ID)	3	−3452.98	6912	13.73	0	0	0.54

*ΔAICc > 2 indicates a significant difference between two models. R^2m indicates the proportion of variance of the response variable explained by the fixed factor and R^2c indicates the proportion of variance explained by the entire model. The bold values indicate the dependent variables of each model. *Indicates the best model. N = 20 individuals.*

TABLE 3 | *Post-hoc* tests for the song response variables where a best model with at least one fixed factor was selected.

Best model	Estimate	Std. error	*z*-value	Pr(>| z|)
Number of syllables ~ Playback + (1| D)				
Elaborate–Pre playback*	−0.1	0.04	−2.54	0.029
Simple–Pre playback	−0.03	0.04	−0.81	0.69
Simple–Elaborate	0.07	0.03	2.14	0.08
Minimum frequency (Hz) ~ Playback + Order + (1| ID)				
Elaborate–Pre playback*	−220.53	81.35	−2.71	0.017
Simple–Pre playback	−122.03	85.95	−1.42	0.32
Simple–Elaborate	98.5	45.14	2.18	0.07
Frequency bandwidth (Hz) ~ Playback + Order + (1| ID)				
Elaborate–Pre playback*	451.4	129.46	3.49	< 0.01
Simple–Pre playback	235.47	136.76	1.72	0.19
Simple–Elaborate*	−215.93	71.82	−3.01	< 0.01
Maximum frequency (Hz) ~ Playback + Order + (1| ID)				
Elaborate–Pre playback	228.9	105.9	2.16	0.07
Simple–Pre playback	112.5	111.8	1.01	0.56
Simple–Elaborate	−116.5	58.7	−1.98	0.11

**Indicates which pairs of playback periods were statistically distinct in song or behavioral responses. N = 20 individuals.*

minimum frequency to be determined by noise level, and a lower and narrower frequency range was correlated with less elaborate song. In the current experimental study, however, we found a change in bandwidth dependent on song elaboration, but song frequency range was not correlated with song elaboration. We believe that this discrepancy requires further exploration of the potential role for ambient noise in signaling bananaquits.

There are two contextual differences in the recording sets that could explain the inconsistency of the correlation: noise level during recordings and whether song was sung in response to playback. In the previous study, we recorded the birds in quiet and also in noisy conditions, while in the current study, we only recorded the birds in relatively quiet moments of the day. As we found the correlation among the song parameters only in the first study, in which noisy conditions were present, we believe that the traffic noise could be causally linked to the presence of that significant correlation. This is another indication that noisy conditions may play a role in song syllable use restriction through noise-dependent bandwidth availability. In the previous study we also only recorded spontaneous songs, while in the current study, we recorded both spontaneous and playback induced songs. However, in the current study, we found no correlation before nor after the playback. We therefore argue that motivational state is not a likely explanation for the lack of correlation between song elaboration and frequency bandwidth in the current study.

The Audibility-Signal Efficiency Trade-Off

The combination of results of the previous observational study (Winandy et al., 2021) and the current playback study allows a new perspective on the signal audibility/efficiency trade-off (Slabbekoorn and Ripmeester, 2008; Gross et al., 2010; Slabbekoorn, 2013). On the one hand, noise-dependent changes in frequency use may improve signal audibility as (1) avoiding low frequencies leaves a larger part of the song unaffected by masking low-frequency traffic noise (Nemeth and Brumm, 2010; Halfwerk et al., 2011); and (2) concentrating sound energy in a spectrally more narrow bandwidth will also improve the signal-to-noise ratio (Hanna et al., 2011). On the other hand, as song elaboration is meaningful to the birds themselves (current study), the correlation between frequency bandwidth and song elaboration under noisy conditions (previous study, Winandy et al., 2021) can be interpreted as evidence for a restriction on signal efficiency by noise-dependent song bandwidth contraction. When this signal audibility/efficiency trade-off is relaxed under relatively quiet conditions, the correlation between song frequency bandwidth and song elaboration apparently also fades.

Few studies have addressed the consequences of this trade-off between signal audibility and signal efficiency under noisy conditions. We here show for bananaquits that the noise-dependent variation in frequency use concerns biologically relevant signal variation, but for general conclusions the trade-off remains to be tested in more species. We especially need to gain insight into whether vocal changes that improve audibility actually yield any benefit to the signaler. We do know for example from a few earlier playback studies that spectral changes potentially driven by masking traffic noise affect response levels and are therefore proven to be biologically relevant (Mockford and Marshall, 2009; Ripmeester et al., 2010; Luther and Derryberry, 2012). However, we have only begun to discover the potential for reduced responsiveness to urban song features, as modified by anthropogenic noise conditions, in a mate choice context (Halfwerk et al., 2011; Huet des Aunay et al., 2014) as well as in a territorial context of male-male communication (Luther and Magnotti, 2014; LaZerte et al., 2017; Phillips and Derryberry, 2018).

CONCLUSION

In the present study, we showed that bananaquits recognize the variation in song elaboration as they respond with syllable adjustment and spectrally distinct songs to the variation in song elaboration in our playback stimuli. As song elaboration was shown in an earlier study to be restricted by noise-dependent song frequency bandwidth, the current results confirm that song adjustments could increase audibility through masking avoidance, but at the same time affect the signaling function. This provides another example of how the rise in anthropogenic noise levels in avian habitat may not only affect what birds sing, but also what they communicate. We still have little insight into fitness consequences of masking avoidance and changes of noise-induced adjustments in signaling content. We therefore believe that more studies are warranted into human impact on the ecology and evolution of singing birds in their acoustically altered environments due to noisy human activities worldwide.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

The animal study was reviewed and approved by the local 'Committee of Ethics in the Use of Animals', Federal University of Bahia-UFBA, Brazil (n^{TM}36/2016).

AUTHOR CONTRIBUTIONS

GW collected and analyzed the data and constructed the figures. All authors contributed equally to the conception and writing of the manuscript.

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REFERENCES

Barber, J. R., Crooks, K. R., and Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol. Evol.* 25, 180–189. doi: 10.1016/j.tree.2009.08.002

Barton, K. (2016). *MuMIn: Multi-Model Inference. R package version 1.15.6.* Available online at: https://cran.r-project.org/web/packages/MuMIn/index.html (accessed November 10, 2018).

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). *lme4: Linear Mixed-Effects Models Using Eigen and S4. R package version* 1.1-9. Available online at: https://cran.r-project.org/web/packages/lme4/index.html (accessed November 10, 2018).

Bermúdez-Cuamatzin, E., Ríos-Chelén, A. A., Gil, D., and Macías Garcia, C. (2011). Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biol. Lett.* 7, 36–38. doi: 10.1098/rsbl.2010.0437

Botero, C. A., Boogert, N. J., Vehrencamp, S. L., and Lovette, I. J. (2009). Climatic patterns predict the elaboration of song displays in mockingbirds. *Curr. Biol.* 19, 1151–1155. doi: 10.1016/j.cub.2009.04.061

Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* 73, 434–440. doi: 10.1111/j.0021-8790.2004.00814.x

Brumm, H., and Slabbekoorn, H. (2005). Acoustic communication in noise. *Adv. Study Behav.* 35, 151–209.

Brumm, H., Zollinger, S. A., Niemelä, P. T., and Sprau, P. (2017). Measurement artefacts lead to false positives in the study of birdsong in noise. *Methods Ecol. Evol.* 8, 1617–1625. doi: 10.1111/2041-210x.12766

Buchanan, K. L., and Catchpole, C. K. (1997). Female choice in the sedge warbler Acrocephalus schoenobaenus multiple cues from song and territory quality. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 264, 521–526.

Buchanan, K. L., and Catchpole, C. K. (2000). Song as an indicator of male parental effort in the sedge warbler. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 267, 321–326. doi: 10.1098/rspb.2000.1003

Burnham, K. P., and Anderson, D. R. (2002). *A Practical Information-Theoretic Approach: Model Selection and Multimodel Inference*, 2nd Edn. New York, NY: Springer.

Buxton, R. T., McKenna, M. F., Mennitt, D., Fristrup, K., Crooks, K., Angeloni, L., et al. (2017). Noise pollution is pervasive in U.S. protected areas. *Science* 356, 531–533. doi: 10.1126/science.aah4783

Collins, S. (2004). "Vocal fighting and flirting: the functions of birdsong," in *Nature's Music: the Science of Birdsong*, eds P. Marler and H. Slabbekoorn (San Diego, CA: Academic Press), 33–79.

Derryberry, E. P., Gentry, K., Derryberry, G. E., Phillips, J. N., Danner, R. M., Danner, J. E., et al. (2017). White-crowned sparrow males show immediate flexibility in song amplitude but not in song minimum frequency in response to changes in noise levels in the field. *Ecol. Evol.* 7, 4991–5001. doi: 10.1002/ece3.3037

Fouda, L., Wingfield, J. E., Fandel, A. D., Garrod, A., Hodge, K. B., Rice, A. N., et al. (2018). Dolphins simplify their vocal calls in response to increased ambient noise. *Biol. Lett.* 14:20180484. doi: 10.1098/rsbl.2018.0484

Gentry, K. E., McKenna, M. F., and Luther, D. A. (2017). Evidence of suboscine song plasticity in response to traffic noise fluctuations and temporary road closures. *Bioacoustics* 27, 165–181. doi: 10.1080/09524622.2017.1303645

Gil, D., Honarmand, M., Pascual, J., Pérez-Mena, E., and Garcia, C. M. (2014). Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behav. Ecol.* 26, 435–443. doi: 10.1093/beheco/aru207

Gross, K., Pasinelli, G., and Kunc, H. P. (2010). Behavioral plasticity allows short-term adjustment to a novel environment. *Am. Nat.* 176, 456–464. doi: 10.1086/655428

Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., ten Cate, C., et al. (2011). Low-frequency songs lose their potency in noise urban conditions. *Proc. Natl. Acad. Sci. U.S.A.* 108, 14549–14554. doi: 10.1073/pnas.1109091108

Hanna, D., Blouin-Demers, G., Wilson, D. R., and Mennill, D. J. (2011). Anthropogenic noise affects song structure in red-winged blackbirds (*Agelaius phoeniceus*). *J. Exp. Biol.* 214, 3549–3556. doi: 10.1242/jeb.060194

Hasselquist, D., Bensch, S., and von Schantz, T. (1996). Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* 381, 229–232. doi: 10.1038/381229a0

Hilty, S., and Christie, D. A. (2018). "Bananaquit (Coereba flaveola)," in *Handbook of the Birds of the World Alive*, eds J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana (Barcelona: Lynx Edicions).

Hof, D., and Podos, J. (2013). Escalation of aggressive vocal signals: a sequential playback study. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 280:20131553. doi: 10.1098/rspb.2013.1553

Horn, A. G., Leonard, M. L., Ratcliffe, L., Shackleton, S. A., and Weisman, R. G. (1992). Frequency variation in songs of black-capped chickadees (*Parus atricapillus*). *Auk* 109, 847–852. doi: 10.2307/4088158

Huet des Aunay, G., Slabbekoorn, H., Nagle, L., Passas, F., Nicolas, P., and Draganoiu, T. I. (2014). Urban noise undermines female sexual preferences for low-frequency songs in domestic canaries. *Anim. Behav.* 87, 67–75. doi: 10.1016/j.anbehav.2013.10.010

Kagawa, H., and Soma, M. (2013). Song performance and elaboration as potential indicators of male quality in Java sparrows. *Behav. Process.* 99, 138–144. doi: 10.1016/j.beproc.2013.07.012

Kipper, S., Mundry, R., Sommer, C., Hultsch, H., and Todt, D. (2006). Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. *Anim. Behav.* 71, 211–217. doi: 10.1016/j.anbehav.2005.04.011

Langemann, U., Tavares, J. P., Peake, T. M., and McGregor, P. K. (2000). Response of great tits to escalating patterns of playback. *Behaviour* 137, 451–471. doi: 10.1163/156853900502178

Lattin, C., and Ritchison, G. (2009). Intra- and intersexual functions of singing by male blue grosbeaks: the role of within-song variation. *Wilson J. Ornithol.* 121, 714–721. doi: 10.1676/09-026.1

LaZerte, S. E., Slabbekoorn, H., and Otter, K. A. (2016). Learning to cope: vocal adjustment to urban noise is correlated with prior experience in black-capped chickadees. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 283:20161058. doi: 10.1098/rspb.2016.1058

LaZerte, S. E., Slabbekoorn, H., and Otter, K. A. (2017). Territorial black-capped chickadee males respond faster to high-than to low-frequency songs in experimentally elevated noise conditions. *PeerJ* 5:e3257. doi: 10.7717/peerj.3257

Leitão, A., Ten Cate, C., and Riebel, K. (2006). Within-song complexity in a songbird is meaningful to both male and female receivers. *Anim. Behav.* 71, 1289–1296. doi: 10.1016/j.anbehav.2005.08.008

Linhart, P., and Fuchs, R. (2015). Song pitch indicates body size and correlates with males' response to playback in a songbird. *Anim. Behav.* 103, 91–98. doi: 10.1016/j.anbehav.2015.01.038

Linhart, P., Jaška, P., Petrusková, T., Petrusek, A., and Fuchs, R. (2013). Being angry, singing fast? Signalling of aggressive motivation by syllable rate in a songbird with slow song. *Behav. Process.* 100, 139–145. doi: 10.1016/j.beproc.2013.06.012

Linhart, P., Slabbekoorn, H., and Fuchs, R. (2012). The communicative significance of song frequency and song length in territorial chiffchaffs. *Behav. Ecol.* 23, 1338–1347. doi: 10.1093/beheco/ars127

Luther, D. A., and Derryberry, E. P. (2012). Birdsongs keep pace with city life: changes in song over time in an urban songbird affects communication. *Anim. Behav.* 83, 1059–1066. doi: 10.1016/j.anbehav.2012.01.034

Luther, D. A., and Magnotti, J. (2014). Can animals detect differences in vocalizations adjusted for anthropogenic noise? *Anim. Behav.* 92, 111–116. doi: 10.1016/j.anbehav.2014.03.033

Luther, D. A., Phillips, J., and Derryberry, E. P. (2016). Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. *Behav. Ecol.* 27, 332–340. doi: 10.1093/beheco/arv162

Mennitt, D. J., Fristrup, K. M., and Nelson, L. (2015). A spatially explicit estimate of environmental noise exposure in the contiguous United States. *J. Acoust. Soc. Am.* 137, 2339–2340. doi: 10.1121/1.4920539

Mockford, E. J., and Marshall, R. C. (2009). Effects of urban noise on song and response behaviour in great tits. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 276, 2979–2985. doi: 10.1098/rspb.2009.0586

Montague, M. J., Danek-Gontard, M., and Kunc, H. P. (2012). Phenotypic plasticity affects the response of a sexually selected trait to anthropogenic noise. *Behav. Ecol.* 24, 343–348. doi: 10.1093/beheco/ars169

Morton, E. S., and Young, K. (1986). A previously undescribed method of song matching in a species with a single song 'type', the Kentucky warbler (*Oporornis formosus*). *Ethology* 73, 334–342. doi: 10.1111/j.1439-0310.1986.tb00813.x

Moseley, D. L., Phillips, J. N., Derryberry, E. P., and Luther, D. A. (2019). Evidence for differing trajectories of songs in urban and rural populations. *Behav. Ecol.* 30, 1734–1742. doi: 10.1093/beheco/arz142

Nakagawa, S., and Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142. doi: 10.1111/j.2041-210x.2012.00261.x

Nelson, D. A. (1988). Feature weighting in species song recognition by the field sparrow (*Spizella pusilla*). *Behaviour* 106, 158–182. doi: 10.1163/156853988x00142

Nemeth, E., and Brumm, H. (2010). Birds and anthropogenic noise: Are urban songs adaptive? *Am. Nat.* 176, 465–475. doi: 10.1086/656275

Otter, K. A., Ratcliffe, L., Njegovan, M., and Fotheringham, J. (2002). Importance of frequency and temporal song matching in black-capped chickadees: evidence from interactive playback. *Ethology* 108, 181–191. doi: 10.1046/j.1439-0310.2002.00764.x

Parris, K. M., and McCarthy, M. A. (2013). Predicting the Effect of Urban Noise on the Active Space of Avian Vocal Signals. *Am. Nat.* 182, 452–464. doi: 10.1086/671906

Phillips, J. N., and Derryberry, E. P. (2017). Equivalent effects of bandwidth and trill rate: support for a performance constraint as a competitive signal. *Anim. Behav.* 132, 209–215. doi: 10.1016/j.anbehav.2017.08.012

Phillips, J. N., and Derryberry, E. P. (2018). Urban sparrows respond to a sexually selected trait with increased aggression in noise. *Sci. Rep.* 8:7505.

Pohl, N. U., Leadbeater, E., Slabbekoorn, H., Klump, G. M., and Langemann, U. (2012). Great tits in urban noise benefit from high frequencies in song detection and discrimination. *Anim. Behav.* 83, 711–721. doi: 10.1016/j.anbehav.2011.12.019

Potvin, D. A., and Mulder, R. A. (2013). Immediate, independent adjustment of call pitch and amplitude in response to varying background noise by silvereyes (*Zosterops lateralis*). *Behav. Ecol.* 24, 1363–1368. doi: 10.1093/beheco/art075

Rabin, A. L., and Greene, C. M. (2002). Changes to acoustic communication systems in human-altered environments. *J. Comp. Psychol.* 116, 137–141. doi: 10.1037/0735-7036.116.2.137

Reichard, D. G., Rice, R. J., Vanderbilt, C. C., and Ketterson, E. D. (2011). Deciphering information encoded in birdsong: male songbirds with fertile mates respond most strongly to complex, low-amplitude songs used in courtship. *Am. Nat.* 178, 478–487. doi: 10.1086/661901

Riebel, K., Odom, K. J., Langmore, N. E., and Hall, M. L. (2019). New insights from female bird song: towards an integrated approach to studying male and female communication roles. *Biol. Lett.* 15:20190059. doi: 10.1098/rsbl.2019.0059

Ripmeester, E. A., De Vries, A. M., and Slabbekoorn, H. (2007). Do blackbirds signal motivation to fight with their song? *Ethology* 113, 1021–1028. doi: 10.1111/j.1439-0310.2007.01398.x

Ripmeester, E. A. P., Mulder, M., and Slabbekoorn, H. (2010). Habitat-dependent acoustic divergence affects playback response in urban and forest populations of the European blackbird. *Behav. Ecol.* 21, 876–883. doi: 10.1093/beheco/arq075

Searcy, W. A., and Anderson, M. (1986). Sexual selection and theevolution of song. *Annu. Rev. Ecol. Syst.* 17, 507–533.

Searcy, W. A., and Beecher, M. D. (2009). Song as an aggressive signal in songbirds. *Anim. Behav.* 78, 1281–1292. doi: 10.1016/j.anbehav.2009.08.011

Searcy, W. A., and Nowicki, S. (2000). *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton, NJ: The Princeton University Press, 288.

Slabbekoorn, H. (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* 85, 1089–1099. doi: 10.1016/j.anbehav.2013.01.021

Slabbekoorn, H., and Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature* 424, 267–267. doi: 10.1038/424267a

Slabbekoorn, H., and Ripmeester, E. A. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Mol. Ecol.* 17, 72–83. doi: 10.1111/j.1365-294x.2007.03487.x

Slabbekoorn, H., and ten Cate, C. (1996). Responses of collared doves to playback of coos. *Behav. Process.* 38, 169–174. doi: 10.1016/s0376-6357(96)00023-x

Slabbekoorn, H., and ten Cate, C. (1998). Perceptual tuning to frequency characteristics of territorial signals in collared doves. *Anim. Behav.* 56, 847–857. doi: 10.1006/anbe.1998.0887

Verzijden, M. N., Ripmeester, E. A. P., Ohms, V. R., Snelderwaard, P., and Slabbekoorn, H. (2010). Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. *J. Exp. Biol.* 213, 2575–2581. doi: 10.1242/jeb.038299

Winandy, G. S. M. (2019). "Consequences of anthropogenic noise to song elaboration, signal value and reproductive success: field and captive studies in neotropical Bananaquits and Bengalese finches," in *Tese (Doutorado em Psicologia Experimental) – Instituto de Psicologia* (São Paulo: Universidade de São Paulo), 96f.

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Urban Noise Restricts Song Frequency Bandwidth and Syllable Diversity in Bananaquits: Increasing Audibility at the Expense of Signal Quality

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Anthropogenic noise can interfere with animal behavior through masking of acoustic communication. In response to masking, animals may change their acoustic signals as an apparent adjustment strategy, but this may have a drawback on signal quality. Songs and calls may show noise-dependent changes in frequency and duration, which may yield some masking avoidance, but may also constrain other acoustic parameters that might carry information about the sender. In the present study, we investigated whether noise-dependent reduction in frequency bandwidth or song duration restricted syllable diversity or song elaboration in a Neotropical songbird, the bananaquit (*Coereba flaveola*). We show that bananaquits sing higher frequency songs, of narrower bandwidth, in noisier territories, independent of variation in territory density, without significant variation in song duration. We also show that songs with higher minimum frequencies, narrower bandwidths, and shorter durations have on average a lower number of syllable types and higher syllable rates. This finding is in line with an acoustic restriction and may reflect a functional trade-off between audibility and signal value: higher frequencies may be more audible but less elaborate songs may weaken the message of sender quality. Consequently, noise pollution may not only alter avian communities, but also shape acoustic diversity and processes of sexual selection in urban environments.

Keywords: behavioral plasticity, noise-dependent adjustments, song complexity, song quality, song elaboration

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INTRODUCTION

Anthropogenic noise has increased in natural and human-altered habitats (Mennitt et al., 2015; Buxton et al., 2017), where it might negatively affect vocally communicating animals. The elevated noise levels can cause acoustic interference by masking the functional variation in frequency and amplitude of vocal signals, for example in frogs, birds, and mammals (Wollerman and Wiley, 2002; Lohr et al., 2003; Erbe et al., 2016). Acoustic overlap in time and frequency with anthropogenic noise may decrease the detectability and recognizability of animal vocalizations and thereby disrupt or alter communication (Barber et al., 2010; Parris and McCarthy, 2013; Templeton et al., 2016). The masking problems are typically biased to the lower frequencies of animal signals, because anthropogenic noise is biased to lower frequencies (Halfwerk et al., 2011a; Lazerte et al., 2017). As a consequence, anthropogenic noise may negatively impact vocal function and undermine survival and reproductive success (Halfwerk et al., 2011b; Potvin and MacDougall-Shackleton, 2015; Kleist et al., 2018), for example through reduced foraging efficiency while avoiding predation, and less success in territory defense and mate attraction (Quinn et al., 2006; Halfwerk et al., 2011a; Kleist et al., 2016).

Evidence for a detrimental impact of anthropogenic noise via interference of acoustic communication has been reported in a variety of studies. Ambient noise levels may for example affect courtship: female great tits (*Parus major*) and female canaries (*Serinus canaria*) were found to respond less to the low-frequency songs of males in experimentally elevated noisy conditions than in ambient control conditions (Halfwerk et al., 2011a; Huet des Aunay et al., 2014). Ambient noise levels may also undermine communication about predation risk. Savannah sparrows (*Passerculus sandwichensis*) delay feeding visits to their nestlings when hearing conspecific alarm calls or predators. This behavior is likely reducing predation for both parents and nestlings, but feeding latencies declined under noisy conditions despite the presence of alarm calls or predator songs (Antze and Koper, 2018). A solution to the problems, at least to some extent, would be to adjust acoustic signals in such a way that would reduce masking by anthropogenic noise.

Several types of noise-dependent vocal adjustments could make signals more audible under noisy conditions. For bird songs, the vocal adjustments include modifications of the minimum frequency, changes in duration, amplitude and syllable rate, and altered timing of vocal activity (Brumm, 2004; Potvin and Mulder, 2013; Gil et al., 2014). Specifically, city birds have been reported to sing higher-pitched, longer and more intense vocalizations than birds of the same species from more quiet territories in rural areas (Slabbekoorn and Den Boer-Visser, 2006; Brumm and Zollinger, 2011; Ríos-Chelén et al., 2013). Such song adjustments may decrease the masking effect of the typical low-frequencies of anthropogenic noise and increase song audibility (Brumm and Slabbekoorn, 2005; Pohl et al., 2012). Spectral and temporal adjustments, however, could also lead to vocal restrictions on signal efficiency, as they may prevent the use of specific syllables with potentially high signal value (Halfwerk et al., 2011a,b; Huet des Aunay et al., 2014) or reduce available repertoire size, which may also signal some sender quality (Buchanan and Catchpole, 2000; Kipper et al., 2006).

There is indeed some evidence that spectral and temporal shifts under noisy conditions may impose inherent restrictions on syllable diversity. Montague et al. (2012) found that European robins (*Erithacus rubecula*) increased the minimum frequency of their songs in response to an elevation in ambient noise levels, which was associated with a synchronous decrease in frequency bandwidth, song duration and syllable length, as well as a decrease in the number of different syllable types. Montague et al. (2012) argued that birds may respond with adjustments in song structure to masking noise, but that acoustic plasticity may be restricted by mechanistic correlations among different song parameters. If such restrictions to acoustic variety affect song function, birds face a trade-off between audibility and signal quality (Slabbekoorn and Ripmeester, 2008; Gross et al., 2010; Slabbekoorn, 2013; Luther et al., 2016), regardless of whether acoustic changes are a direct response to elevated noise levels, or an indirect consequence of a noise-dependent change in another parameter.

Song frequency use or syllable diversity may also be affected by factors other than ambient noise. For some bird species, population density can increase in human-altered habitats due to the increased availability of food resources and decreased presence of predators (Tomiałojć, 1998; Chace and Walsh, 2006; Ciach and Fröhlich, 2017). High territory density may induce competition among males and change their singing behavior (Dabelsteen and Pedersen, 1990; Ripmeester et al., 2010; Narango and Rodewald, 2015). Territory density may therefore be correlated to motivational variation in temporal components of song, such as syllable length, syllable rate, number of syllables and song length (Hamao et al., 2011; Narango and Rodewald, 2015). However, it has also been shown that territorial density can correlate with song frequency use. With higher territory densities, great tits (*Parus major*) were found to sing with higher minimum frequencies (Hamao et al., 2011), and European blackbirds (*Turdus merula*) were found to sing with higher peak frequencies (Ripmeester et al., 2010). Therefore, territory density, varying between urban and rural populations, may be an alternative explanation for noise-dependent song variation and thereby a confounding variable that should be taken into account.

The neotropical songbird bananaquit (*Coereba flaveola*) is an excellent model system to study noise-dependent song variation and to test for potential signaling trade-offs due to inherent acoustic correlations among song parameters. Bananaquits exhibit quite complex vocalizations, including relatively large song repertoires and high singing rates (Wunderle et al., 1992), a variety of high- and low-pitched syllable types, while song diversity and elaboration has been reported to vary among birds from different areas (Hilty and Christie, 2018). Furthermore, they are relatively abundant and have urban and rural distributions where they breed and sing in a variety of microhabitats with variable ambient noise levels. The bananaquit is typically also used to human presence and thereby very suitable to approach for song recordings and analyses of geographic variation and correlation to environmental variables.

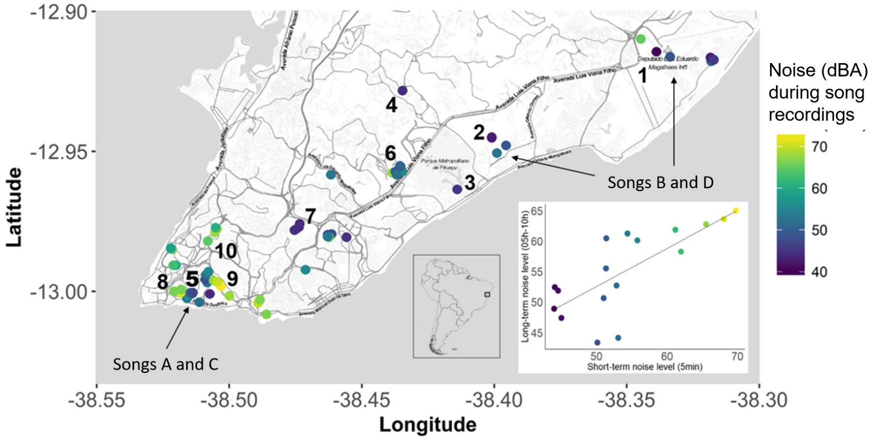

FIGURE 1 | Map representing the distribution of the recorded birds in the city of Salvador, Bahia, Brazil, and the variation of noise levels along sampled territories and in the correlational graph (long-term and short-term noise recordings). The color of the dots represents the intensity of the environmental noise (in decibels, A-curve), measured during the recording of bananaquit songs. In a continuous colored scale, purple dots represent quieter territories and yellow dots the noisier territories. Indicated by numbers are example of quieter and noisier localities and their respective habitat types: Tropical sand dunes of (1) "Parque da Dunas," Atlantic forest fragments of (2) "Vale Encantado," (3) "Parque de Pituaçu," (4) "Jardim Botânico," (5) "Parque Zoobotânico Getúlio Vargas", and (6) "Coelba," Urban Gardens of (7) "Jardim da Saudade," and (8) Federal University of Bahia; Main avenues in (6) "Coelba," (9) "Garibaldi," and (10) "Dique." Map made with ggmap package (Kahle and Wickham, 2013).

In this study, we recorded bananaquit songs in urban territories with variable ambient noise levels to correlate song variation to noise, taking territory density into account. We aimed to answer the following questions: (1) do bananaquit songs have higher minimum and maximum frequencies, do they have narrower frequency bandwidths, and are their songs shorter, in noisier territories? (2) is territory density a confounding variable and also correlated to song frequency use or duration? and (3) does any potential noise-dependent song structure restrict song elaboration, yielding less and lower diversity in syllables? If so, we would provide more insight into how noise pollution may alter conditions for sexual selection and evolutionary change in urban bird species, as well as shape species and song diversity of urban bird communities.

MATERIALS AND METHODS

Subject Species and Study Area

Bananaquits (*Coereba flaveola*) are small nectivorous birds with a downward curved bill that occur across the Neotropics, from Southern Mexico to Northern Argentina and the Caribbean islands. They breed in a wide variety of habitats, predominantly at low elevation, including city gardens, urban parks, disturbed areas, and forest borders, in which they can experience a variety of high and low traffic loads (Hilty and Christie, 2018). They are largely monomorphic and appear in the study area with a gray back, black crown and cheek, white eyebrow, light-gray throat, and a bright yellow belly (this plumage varies geographically). Bananaquits are persistent singers and breed throughout the year (Hilty and Christie, 2018). The song is a relatively short series of high-pitched syllables, with more or less repeated sound elements that are often repeated in stereotypic fashion. They can sing during all parts of the day, including the rush hours (personal observation). Their high singing rate comes together with large song repertoires of 120 –340 songs per male, which are mostly produced by the addition and/or deletion of notes at the end of the songs (Wunderle et al., 1992). Although each male is able to produce large amounts of song variation, territory neighbors hardly share similar song types (Wunderle et al., 1992).

We conducted our study in urban parks and built-up areas in the city of Salvador, Bahia, Brazil, between January of 2016 and March of 2018. We visited localities 400 m to 25 km apart (**Figure 1**). Our sampling covered a range of environmental noise levels from 40 to 73 decibels (dBA). We recorded bananaquits, for example, in the relatively quiet areas of the tropical sand dunes ("restinga") of "Parque das Dunas," at the borders of the Atlantic forest fragments of "Jardim Botânico," "Parque de Pituaçu," "Vale Encantado," and "Parque Zoobotânico Getúlio Vargas," and in urban gardens of "Jardim da Saudade" and the Federal University of Bahia. Noisier bananaquit territories were recorded in busier, urban areas—i.e., main avenues with high concentration of concrete buildings and low quantities of natural trees and gardens—which occur alongside Atlantic forest fragments, such as "Coelba," at the borders of the sand dunes, and in urban gardens such as at the "Garibaldi," and "Dique" localities. We consider our sampling design as a contiguous population in urbanized area with high heterogeneity in terms of vegetation, buildings and noise level. All territories, localities and respective ambient noise levels are represented in the map (**Figure 1**), which was generated using "ggmap" packge in R TM software (Kahle and Wickham, 2013).

Song Recordings and Noise Measurements

We recorded bananaquit songs with a Sennheiser TM (Wedemark, Germany) shotgun directional microphone (ME67 + K6) connected to a Sony TM (Tokyo, Japan) PCM-D50 digital recorder. Song recordings were taken in WAV format, at a sampling rate of 44.1 kHz. We recorded the birds mostly between 05:00 and 10:00, from a distance of 5–10 m to the focal bird, and each bird was recorded only once. To improve signal-to-noise ratio and the quality of the recordings in noisy locations, we positioned the microphone as close as possible to the bird and as far as possible from the noise source. We positioned the direction of the microphone in parallel to the direction of the noise source as the sides of the microphone are the least sensitive. Additionally, we positioned a barrier, like a car or a wall, between the noise source and the microphone when possible (c.f. Slabbekoorn, 2012).

We measured the ambient noise level in each territory where we were able to record sufficient bananaquit songs. We assessed the sound levels of ambient noise for 5 min, starting at the beginning of song recording, using a sound pressure level meter with data logger Skill-Tec TM (São Paulo, São Paulo, Brazil) SKDEC–02 (A-weighting, slow response, range 30–130 dB, 1s interval). We positioned the equipment upwards, kept vertically on a tripod at 150 cm from the ground. The 5 min sample was integrated into a single, average sound level (dBA) as the ambient noise measure per territory.

The variation in sound levels within territories across the time period of sampling may undermine comparisons across territories (Slabbekoorn and Peet, 2003; Arroyo-Solís et al., 2013). This potential problem was checked with repeated sound level measurements over the morning in a subset of bananaquit territories. We averaged 10–5 min samples per locality recorded between 05:00 and 10:00, sampled at the start of each half hour. These long-term averages were compared to the nearest short-term territory samples by a simple regression, where the long-term averages represented the independent variable and the nearest short-term samples the dependent variable.

Song Processing and Measurements

The song recordings were high-pass filtered between 0.5 and 2.5 kHz using the software Audacity TM v. 2.1.2 (Carnegie Mellon University, Pittsburgh, Pennsylvania, United States). We used spectrogram observation to adjust filter limits for each individual recording, to remove as much ambient noise as possible, without removing any trace of song. The omission of low-frequency background noise renders a distinct presence of the target songs in the amplitude wave, which supported the measurement of song duration on the spectrogram. We generated song spectrograms and waveforms with Raven TM PRO software (Cornell Laboratory of Ornithology, Ithaca, NY, United States) version 1.5. The chosen parameters for the calculation of spectrograms were Hann windows, DFT size 512 samples, and an overlap of 50%.

We measured spectral and temporal variables for each song of a bout of a total of 1 –13 songs per individual. The spectral and temporal song parameters were: minimum, maximum and peak frequency ($\log_{10}$Hz), frequency bandwidth ($\log_{10}$Hz) and song duration (s). We assessed these measures by cursor placement and the automated writing to file procedure of the Raven TM PRO software. There are advantages and disadvantages to the method of cursor placement compared to a fully objective automated measurement technique by amplitude cut-off points relative to the peak amplitude in the song (Verzijden et al., 2010; Zollinger et al., 2012; Ríos-Chelén et al., 2016). The potential issues about effect and artifact size are addressed in the discussion (c.f. Verzijden et al., 2010). We $\log_{10}$ transformed the frequency measurements for each recorded song, before performing any averages (for the graphics) and statistical analyses, as this better reflects pitch perception in birds and should therefore provide a biologically more relevant *t*-test (Cardoso, 2013). For frequency bandwidth ($\log_{10}$Hz), we first log-transformed maximum and minimum frequency measurements and then computed frequency bandwidth as the difference between the two.

An observer bias is possible to some extent for some of the measurements (e.g., minimum and maximum frequency), as we had clear directional expectations about noise-dependent song variation (c.f. Brumm et al., 2017). However, our recording strategy in the field, to optimize signal-to-noise ratio, reduced direct audibility of current noise level during song measurements. Furthermore, noise level fluctuations in time also reduced the link between noise conditions at specific recording times and average noise levels. Consequently, song analyses were largely blind to variation in the relative noise level among territories, which should prevent problems of observer bias.

We also quantified four measurements of song elaboration, related to the number of repeated song units and the acoustic variety among these units, as done in several studies for different species (Garamszegi and Moller, 2004; Soma and Garamszegi, 2011; Hill et al., 2017). Also the measurements were done for each song of a bout of 1–13 songs per individual. We quantified: (1) number of syllables (sound units per song), (2) number of syllable types (different sound units per song), (3) syllable rate (number of syllables sung per second); and (4) number of phrases. Phrases in bananaquits may concern trills formed by repetitions of the same syllable, fixed combinations of note complexes, or stereotypic sequences of different syllables (Thompson et al., 1994). These measures of song elaboration have been shown to play a role in communication related to sexual and territorial advertisement (Hoi-Leitner et al., 1995; Catchpole and Leisler, 1996; Soma and Garamszegi, 2011; Hill et al., 2017).

Territory Density Assessment

We assessed the number of singing bananaquits within a range of 100 m of a target territory. Within this distance, birds are expected to properly hear each other and face relevant territorial interactions (Ripmeester et al., 2010; Hamao et al., 2011; Narango and Rodewald, 2015). Bananaquits may hear more neighbors than human observers, due to a perceptual focus on conspecific song features and advantageous perch heights. However, it is important to have a measure of territory density that is sampled in a standardized way and which adequately reflects variation among territories in density related competition.

Statistical Analysis

We tested whether spectral and temporal song measurements (minimum, maximum, peak frequency, frequency bandwidth and song duration) were influenced by the noise level measures

TABLE 1 | Fitted linear mixed models of the spectral or temporal or elaboration song variables on the noise level.

Song variables	Estimate	Std. Error	*t*-value	*P*-value	R2m	R2c
Low frequency ($\log_{10}$Hz)	0.0069	0.0011	6.02	**<0.001**	0.306	0.74
High frequency ($\log_{10}$Hz)	0.0007	0.0002	2.64	**0.01**	0.066	0.51
Frequency bandwidth ($\log_{10}$Hz)	−0.0061	0.0011	−5.44	**<0.001**	0.255	0.69
Peak frequency ($\log_{10}$Hz)	0.0004	0.0007	0.53	0.59	0.002	0.38
Song duration (s)	−0.0041	0.0083	−0.49	0.62	0.001	0.29
Number of syllables	0.0024	0.0037	0.66	0.5	0.003	0.39
Number of syllable types	−0.005	0.0033	−1.58	0.11	0.012	0.85
Number of phrases	0.022	0.013	1.66	0.10	0.026	0.46
Syllable rate	0.023	0.016	1.37	0.17	0.023	0.67

Individuals are included as a random factor. We provide coefficient values, t statistics, significance values, multiple R squared, and adjusted R squared values. In bold are the p-values for significant results (N = 65).

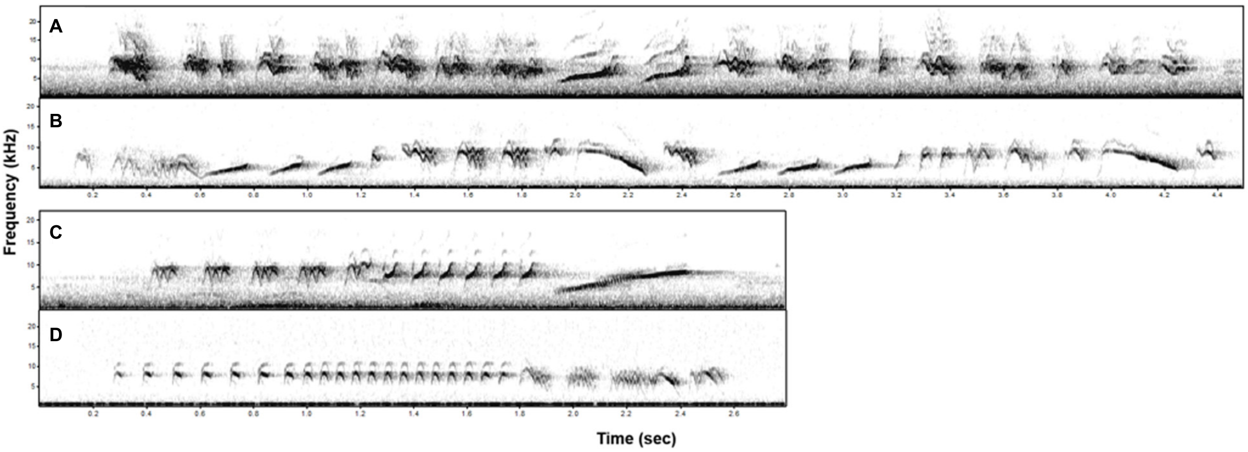

FIGURE 2 | Spectrograms of four bananaquit songs differing in levels of elaboration, i.e., in the number of different syllable types. More **(A,B)** and less **(C,D)** elaborate songs occur both in the most geographically distant locations.

associated with individual song recordings. We also tested for a confounding impact by social competition by interplaying these spectral, temporal and elaboration song measurements to territory density. Finally, we tested whether the noise-dependent spectral variation in songs found in the first tests affected the song elaboration. We added song duration as a covariate to these analyses, as song duration can affect our measures of song elaboration. We used linear mixed models (LMM) throughout by selecting the "lme4" function (Bates et al., 2015) of R software (R Core Team, 2017). Each model contained one spectral, temporal or elaboration song measurement as the dependent variable, noise or territory density as independent variable, and individual as a random factor. To test the interplay between song spectral measurements and song elaboration, each model contained one elaboration measurement of the song as the dependent variable (syllable types, number of syllables, number of phrases and syllable rate), one spectral characteristic of the songs and song duration as covariate independent variables (minimum, maximum frequency and frequency bandwidth), and individual as a random factor. For ordinal variables as number of syllables, we used a Poisson distribution and for numeric variables as spectral and temporal measurements, we used a Gaussian distribution. Using the same software and "lme4" function, we performed linear mixed models to investigate whether there was an interplay between the spectral variables minimum, maximum frequency and frequency bandwidth, the number of neighbors, song duration, and the song elaboration measurements.

RESULTS

We recorded songs and assessed ambient noise levels in 65 bananaquit territories and measured the territory density of 37 of these in terms of the number of singing male neighbors audible to the human observer. Three out of four of the spectral song measurements were significantly related to the ambient noise level. Song minimum and maximum frequencies were higher in noisier territories, with noise-related differences in minimum frequency being more prominent than differences in maximum frequency (**Table 1** and **Figures 2**, **3**). As a consequence, we found that also the frequency bandwidth was significantly related to noise level, with a narrower frequency range in noisier conditions (**Table 1**). Peak frequency and song duration were not influenced by the noise level (**Table 1**). The spectral, temporal and

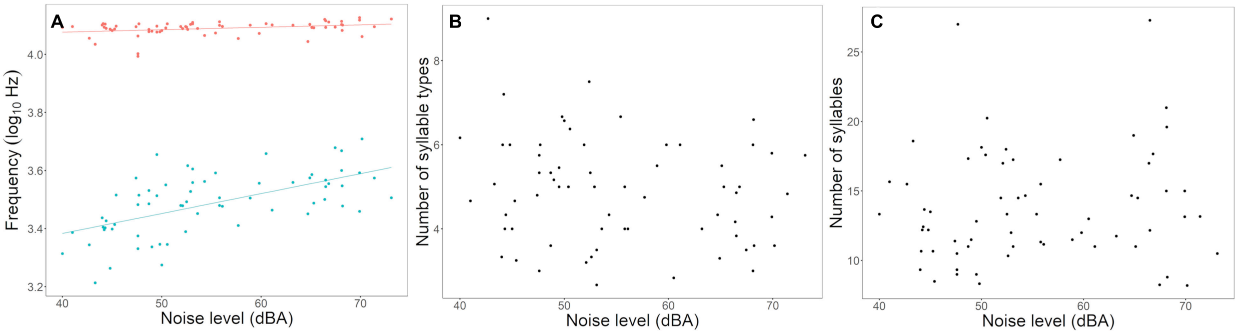

FIGURE 3 | Relationship between noise level and bananaquit song variables. In noisier situations, bananaquits sing higher songs **(A)**, do not change the song syllable length **(B)**, nor the syllable diversity **(C)**. The lines represent the fitted linear model for significant results. In graph A, blue lines and dots represent the minimum frequency and the red line and dots represent the maximum frequency.

TABLE 2 | Fitted linear mixed models of the spectral or temporal or elaboration song variables on the bird density.

Song variables	Estimate	Std. Error	*t-/z*-value	*P*-value	R2m	R2c
Low frequency ($\log_{10}$Hz)	0.014	0.016	0.88	0.37	0.012	0.63
High frequency ($\log_{10}$Hz)	0.0011	0.003	0.28	0.77	0.001	0.69
Frequency bandwidth ($\log_{10}$Hz)	−0.013	0.16	−0.82	0.41	0.010	0.61
Peak frequency ($\log_{10}$Hz)	0.013	0.011	1.26	0.215	0.015	0.23
Song duration (s)	−0.284	0.225	−1.25	0.215	0.026	0.77
Number of syllables	−0.095	0.063	−1.51	0.132	0.033	0.60
Number of syllable types	−0.032	0.062	−0.529	0.596	0.002	0.22
Number of phrases	−0.094	0.071	−1.318	0.187	0.016	0.12
Syllable rate	−0.095	0.180	−0.531	0.598	0.004	0.79

Individuals are included as a random factor. Bird density is represented by the number of singing neighbors (N = 37).

elaboration variables that were related to the ambient noise level were not related to territory density (**Table 2**). The short-term noise measurements, sampled in a 5-min period during song recordings, associated well with the long-term noise assessments, based on ten 5-mi periods spread out over the 5-h period of song recordings between 5.00 and 10.00 h in the morning ($r2 = 0.5598$, $t = 4.367$, $p = 0.0005$, $N = 17$, **Figure 1**).

The frequency variation in minimum frequency and frequency bandwidth and also song duration were significantly related to measures of song elaboration (**Table 3**). The minimum song frequency was negatively correlated to the number of different syllable types, while the frequency bandwidth and song duration were positively related to the number of syllable types. This means that a narrower frequency bandwidth, driven by a higher minimum frequency, together with a shorter duration, lead to less syllable diversity (**Table 3** and **Figure 4**). The minimum and maximum song frequency were positively related, and the frequency bandwidth and song duration negatively related to syllable rate. This means that songs with higher minimum and maximum frequencies had a narrower frequency bandwidth and shorter duration, which yielded higher rates of syllables sang per second (**Table 3** and **Figure 4**). Finally, spectral measurements did not correlate to the number of syllables or phrases. Here, song duration was just related to the number of syllables and phrases. This means that shorter songs naturally had less total number of syllables and phrases.

DISCUSSION

We investigated whether bananaquit songs exhibited noise-dependent variation in spectral and temporal parameters and whether higher minimum song frequencies, narrower frequency bandwidths, or shorter songs would restrict song elaboration. Bananaquit songs varied spectrally with noise levels among individuals from different territories, but song duration did not. We found significantly higher minimum and maximum frequencies and significantly narrower frequency bandwidth in noisier territories. The elevated minimum song frequency was more prominent than the noise-dependent maximum frequency, which is in line with a masking avoidance strategy against traffic noise biased to low frequencies. The noise-dependent spectral variation was not affected by territory density, and appears to restrict song elaboration. Despite being not related to the noise levels, song duration was related to frequency bandwidth and song elaboration: higher, narrower, and shorter songs showed less diversity in the number of different syllable types in a song.

Trade-Off Between Audibility and Signal Quality

The noise-dependent changes in frequencies can make bananaquit songs more audible under noisy conditions, but at the same time make them of lower signal value to the singer

TABLE 3 | Fitted linear mixed models of the elaboration song measurements on the spectral song variables and song duration.

Models	Independent variable	Estimate	Std. Error	*t*-value	*P*-value	R2m	R2c
Number of syllable types ~ Minimum frequency ($\log_{10}$Hz) + Song duration (1| ID)	Minimum frequency ($\log_{10}$Hz)	−3.3893	0.815	−4.115	**<0.001**	0.276	0.551
	Song duration	0.7311	0.081	8.926	**<0.001**	0.276	0.551
Number of syllable types ~ Maximum frequency ($\log_{10}$Hz) + Song duration + (1| ID)	Maximum frequency ($\log_{10}$Hz)	−0.742	2.926	−0.254	0.800	0.0009	0.44
	Song duration	0.77	0.083	9.252	**<0.001**	0.192	0.555
Number of syllable types ~ Frequency bandwidth ($\log_{10}$Hz) + song duration + (1| ID)	Frequency bandwidth ($\log_{10}$Hz)	4.627	1.963	2.357	**0.019**	0.219	0.552
	Song duration	0.737	0.083	8.820	**<0.001**	0.219	0.552
Number of syllables ~ Minimum frequency ($\log_{10}$Hz) + song duration + (1| ID)	Minimum frequency ($\log_{10}$Hz)	3.01	1.716	1.753	0.08	0.675	0.888
	Song duration	5.08	0.15	33.327	**<0.001**	0.675	0.888
Number of syllables ~ Maximum frequency ($\log_{10}$Hz) + song duration + (1| ID)	Maximum frequency ($\log_{10}$Hz)	−0.073	5.51	−0.013	0.989	0.67	0.88
	Song duration	5.049	0.15	33.04	**<0.001**	0.67	0.88
Number of syllables ~ Frequency bandwidth ($\log_{10}$Hz) + song duration + (1| ID)	Frequency bandwidth ($\log_{10}$Hz)	−4.201	3.83	−1.097	0.27	0.674	0.886
	Song duration	5.076	0.15	32.993	**<0.001**	0.674	0.886
Number of phrases ~ Minimum Frequency ($\log_{10}$Hz) + song duration + (1| ID)	Minimum frequency ($\log_{10}$Hz)	0.980	0.657	1.491	0.137	0.298	0.612
	Song duration	0.786	0.063	12.317	**<0.001**	0.298	0.612
Number of phrases ~ Maximum frequency ($\log_{10}$Hz) + song duration + (1| ID)	Maximum frequency ($\log_{10}$Hz)	2.039	2.242	0.909	0.364	0.291	0.619
	Song duration	0.768	0.063	12.070	**<0.001**	0.291	0.619
Number of phrases ~ Frequency bandwidth ($\log_{10}$Hz) + song duration + (1| ID)	Frequency bandwidth ($\log_{10}$Hz)	−1.644	1.523	−1.080	0.281	0.291	0.612
	Song duration	0.785	0.064	12.21	**<0.001**	0.291	0.612
Syllable rate ~ Minimum frequency ($\log_{10}$Hz) + song duration + (1| ID)	Minimum frequency ($\log_{10}$Hz)	1.719	0.756	2.273	**0.023**	0.031	0.690
	Song duration	−0.188	0.066	−2.833	**0.004**	0.031	0.690
Syllable rate ~ Maximum frequency ($\log_{10}$Hz) + song duration + (1| ID)	Maximum frequency ($\log_{10}$Hz)	8.908	2.368	3.762	**< 0.001**	0.047	0.695
	Song duration	−0.227	0.065	−3.762	**<0.001**	0.047	0.695
Syllable rate ~ Frequency bandwidth ($\log_{10}$Hz) + song duration + (1| ID)	Frequency bandwidth ($\log_{10}$Hz)	−5.212	1.663	−3.134	**0.001**	0.045	0.699
	Song duration	−0.174	0.066	−2.638	**0.008**	0.045	0.699

ID = Individuals as a random factor. PS: Song duration = song duration as a random factor for the model of syllable types ~ log frequency bandwidth. N = 65 individuals; number of obs = 301. In bold are the p-values for the significant results.

(Slabbekoorn, 2013; Luther et al., 2016). Bananaquits sang with higher minimum and maximum frequencies, but as the minimum frequency shift was more prominent, songs also became of narrower frequency bandwidth in noisier territories. The different extents of change in minimum and maximum frequencies makes a mechanistic coupling of noise-dependent amplitude and frequency use (Verzijden et al., 2010) less likely as an explanation for the higher sound frequencies in bananaquit songs from noisy territories (Cardoso and Atwell, 2011). Spectral masking avoidance of low-frequency traffic noise (c.f. Slabbekoorn and Peet, 2003) may therefore be a likely explanation, as, for example, great tit females responded more, and male black-capped chickadees (*Poecile atricapillus*) responded faster, to high than to low frequency songs in noisy situations (Halfwerk et al., 2011a; Lazerte et al., 2017). Furthermore, since bananaquit song repertoires are large and

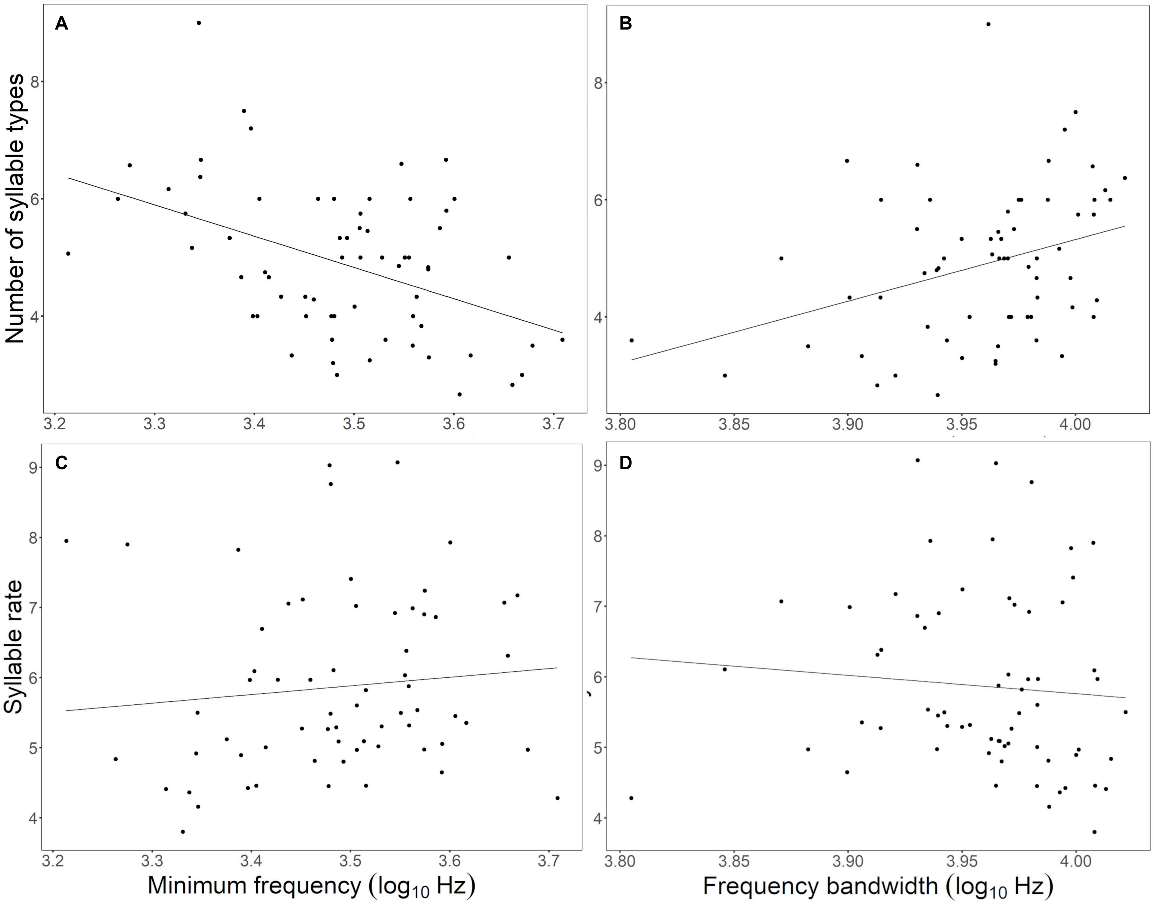

FIGURE 4 | Phenotypic restriction of the song syllable diversity (i.e., number of different syllable types) and syllable rate (i.e., syllables per second) by the increase of the minimum song frequency **(A,B)** and the decrease of the frequency bandwidth **(C,D)**. The black lines represent the fitted linear model for significant results.

versatile, consisting largely of removals or additions of different syllables to the song (Wunderle et al., 1992), it is possible that individuals avoided the masking effect of noise by removing low-frequency syllables from their songs. However, a higher song frequency may also affect signal value, as in some species low-frequency songs have been shown to signal male size and may play a critical role in mate attraction and competitor deterrence (Brown et al., 1996; Linhart et al., 2012; Luther and Magnotti, 2014).

A decrease in frequency bandwidth may also benefit audibility through improvement of signal-to-noise ratio by spectral concentration of signal energy (c.f. Hanna et al., 2011). At the same time, more narrow bandwidths may limit performance features related to combinations of bandwidth and trill rate (c.f. Podos, 1997) and make a song shorter. Songs with restricted bandwidths have also been shown to elicit lower response levels from territorial rivals and to exhibit lower vocal performance than songs with broader frequency bandwidths (Luther et al., 2016; Davidson et al., 2017). For male bananaquits, narrow song bandwidths with short durations, and possibly lower response levels from territorial neighbors (Winandy et al., 2021), could negatively impact the dynamics of territorial defense, while this species has high levels of intrasexual competition over small territory sizes that are constantly being disputed (Wunderle et al., 1992). These data on the production side of communication indicate that bandwidth reductions may negatively impact signal function and thereby reduce mating opportunities and territory defense efficiency.

On top of the direct consequences of noise-dependent spectral changes, we found a correlated reduction of song elaboration that may also affect signal value. In European robins, a noise-dependent increase in minimum song frequency also correlated to a decrease in the number of different syllable types in a song (Montague et al., 2012). This association of spectral restriction and decline in syllable diversity, now found in multiple species, may be related to an elimination of low-frequency syllables and result from inherent acoustic restrictions due to physical constraints. Alternatively, lower syllable diversity may also emerge through the production of more repetitive trills of the same syllables, as syllable rate increased in songs of narrower frequency bandwidth (as illustrated by the example in **Figure 2** and also see **Figure 4**). The increase in syllable rates could also be explained by the fact that song duration was also related to the song elaboration. Shorter songs may have had higher syllable rates because there was less time for singing the relevant syllables. This could be a counter strategy to cope with noisy conditions in itself (Shannon and Weaver, 1949; Wiley, 1994), as suggested, for noise-dependent repetition rates in chaffinches (*Fringilla coelebs*) of Europe (Brumm and Slater, 2006) and urban silvereyes (*Zosterops lateralis*) of Australia (Potvin and Parris, 2012).

The noise-dependent song variation found for the bananaquits can therefore represent a functional trade-off in several ways. The spectral adjustments and increased redundancy may make their songs more audible in the noisy territories. However, the reduced syllable diversity may also affect perceived repertoire size, which may undermine the abilities of singing bananaquits to signal sender quality (Buchanan and Catchpole, 2000; Kipper et al., 2006). Kagawa and Soma (2013) found for example that larger and heavier Java sparrows (*Lonchura oryzibora*) sang more elaborate songs, i.e., with more note types. Whether a detrimental effect on signal content due to reduced syllable diversity applies to bananaquits remains to be tested and could be done by playback experiments (Winandy et al., 2021).

Methodological Validation

Accurate measurements of noise-dependent song frequency variation may be hindered by the fading song amplitude at spectral extremes and the presence of noise around these same frequencies (Verzijden et al., 2010; Zollinger et al., 2012; Ríos-Chelén et al., 2016). Fully objective automated measurements using amplitude cut-off points, relative to the peak amplitude in the song, avoid this problem but compromise on the assessment of the actual song frequency range. Measurements by cursor placement are the most precise determination of spectral song extremes, but may suffer from observer bias (c.f. Brumm et al., 2017) and may introduce a noise-dependent artifact (Verzijden et al., 2010).

For the current study, we selected spectral measurements by cursor placement and we believe that observer bias is not a problem (see section "Materials and Methods"), as any possible artifact is of a much smaller scale than the effect size in our results. Bananaquit songs show, for example, variation over a range of 3,467 Hz in the minimum frequency between the highest and lowest songs and the noise-dependent shift in this parameter concerns about 1,500 Hz over the sampled range of noise levels, from 40 to 70 dB (A). This is a large effect size compared to other descriptive studies on noise-dependent song variation (Nemeth et al., 2012; Slabbekoorn et al., 2012) and far beyond the artifact size in studies that determined this experimentally for measurements on song playbacks with variable noise levels for chiffchaffs (*Phylloscopus collybita*): 49 Hz (Verzijden et al., 2010), and red-winged blackbirds (*Agelaius phoeniceus*): 615 Hz (Ríos-Chelén et al., 2017).

As a final methodological issue, we here briefly address territory density as a potentially confounding variable. Bird densities may increase in cities, for example, by an increase in the availability of nesting sites and food resources (Shochat, 2004). Higher densities may affect urban song variation through altered levels of interaction and agitation that potentially covary with variation in noise levels (Ripmeester et al., 2010; Hamao et al., 2011; Narango and Rodewald, 2015). It is possible that bananaquit densities are higher in more urbanized (and consequently noisier) areas as the species relies on nectar, a very common resource especially in urban parks with a selection of ornamental flowers (Kaluza et al., 2016). However, high densities of bananaquits can indeed be seen in foraging clusters at particular localities, but this seems less so during singing behavior and territorial defense (personal observations). In our study, we also did not find any relationship between our territory density measure and spectral or elaboration features of bananaquit songs. We therefore consider the noise-dependent song variation to be independent of this potentially confounding factor for our species.

CONCLUSION

Neotropical bananaquits present another case of noise-dependent variation in song frequency use, correlated with a decline in song elaboration. We found that bananaquits sang higher minimum and maximum song frequencies, with most prominent changes in minimum frequencies, and a corresponding narrower frequency range in noisier situations. This noise-dependent song frequency use results in masking avoidance of low-frequency traffic noise at least to some extent. Songs in more noisy territories were also shorter, more repetitive and less diverse in terms of the number of different syllable types, which may reduce signal value for mate attraction and territorial defense. Consequently, these findings are congruent with a functional trade-off in song acoustic structure and suggest that urban birds face a compromise between audibility and signal quality. We believe our findings indicate that anthropogenic noise may not only alter the song features birds sing in urban areas, but that these changes can also affect fundamental processes of sexual selection that may undermine individual fitness and the fate of populations.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this study involved only sound recordings of free ranging animals, in their natural habitats, without any interference of their natural behavior or any kind of manipulation of variables. Therefore, an ethical document was not required in my country.

AUTHOR CONTRIBUTIONS

GW, RF, RS, and RM collected and analyzed the data. GW constructed the figures and tables. All authors contributed equally to the conception and writing of the manuscript.

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REFERENCES

Antze, B., and Koper, N. (2018). Noisy anthropogenic infrastructure interferes with alarm responses in Savannah sparrows (*Passerculus sandwichensis*). *R. Soc. Open Sci.* 5:172168. doi: 10.1098/rsos.172168

Arroyo-Solís, A., Castillo, J. M., Figueroa, E., López−Sánchez, J. L., and Slabbekoorn, H. (2013). Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. *J. Avian Biol.* 44, 288–296. doi: 10.1111/j.1600-048x.2012.05796.x

Barber, J. R., Crooks, K. R., and Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol. Evol.* 25, 180–189. doi: 10.1016/j.tree.2009.08.002

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. doi: 10.18637/jss.v067.i01

Brown, W. D., Wideman, J., Andrade, M. C., Mason, A. C., and Gwynne, D. T. (1996). Female choice for an indicator of male size in the song of the black−horned tree cricket, Oecanthus nigricornis (Orthoptera: Gryllidae: Oecanthinae). *Evolution* 50, 2400–2411. doi: 10.2307/2410708

Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* 73, 434–440. doi: 10.1111/j.0021-8790.2004.00814.x

Brumm, H., and Slabbekoorn, H. (2005). Acoustic communication in noise. *Adv. Stud. Behav.* 35, 151–209.

Brumm, H., and Slater, P. J. (2006). Ambient noise, motor fatigue, and serial redundancy in chaffinch song. *Behav. Ecol. Sociobiol.* 60, 475–481. doi: 10.1007/s00265-006-0188-y

Brumm, H., and Zollinger, S. A. (2011). The evolution of the lombard effect: 100 years of psychoacoustic research. *Behaviour* 148, 1173–1198. doi: 10.1163/000579511x605759

Brumm, H., Zollinger, S. A., Niemelä, P. T., and Sprau, P. (2017). Measurements artefacts lead to false positives in the study of birdsong in noise. *Methods Ecol. Evol.* 8, 1617–1625. doi: 10.1111/2041-210x.12766

Buchanan, K. L., and Catchpole, C. K. (2000). Song as an indicator of male parental effort in the sedge warbler. *Proc. R. Soc. B Bio. Sci.* 267, 321–326. doi: 10.1098/rspb.2000.1003

Buxton, R. T., McKenna, M. F., Mennitt, D., Fristrup, K., Crooks, K., Angeloni, L., et al. (2017). Noise pollution is pervasive in U.S. protected areas. *Science* 356, 531–533. doi: 10.1126/science.aah4783

Cardoso, G. C. (2013). Using frequency ratios to study vocal communication. *Anim. Behav.* 85, 1529–1532. doi: 10.1016/j.anbehav.2013.03.044

Cardoso, G. C., and Atwell, J. W. (2011). On the relationship between loudness and increased snog frequency of urban birds. *Anim. Behav.* 82, 831–836. doi: 10.1016/j.anbehav.2011.07.018

Catchpole, C. K., and Leisler, B. (1996). Female aquatic warblers (*Acrocephalus paludicola*) are attracted by playback of longer and more complicated songs. *Behaviour* 133, 1153–1164. doi: 10.1163/156853996x00341

Chace, J. F., and Walsh, J. J. (2006). Urban effects on native avifauna: a review. *Landsc. Urban Plan.* 74, 46–69. doi: 10.1016/j.landurbplan.2004.08.007

Ciach, M., and Fröhlich, A. (2017). Habitat type, food resources, noise and light pollution explain the species composition, abundance and stability of a winter bird assemblage in an urban environment. *Urban Ecosyst.* 20, 547–559. doi: 10.1007/s11252-016-0613-6

Dabelsteen, T., and Pedersen, S. B. (1990). Song and information about aggressive responses of blackbirds, *Turdus merula*: evidence from interactive playback experiments with territory owners. *Anim. Behav.* 40, 1158–1168. doi: 10.1016/s0003-3472(05)80182-4

Davidson, B. M., Antonova, G., Dlott, H., Barber, J. R., and Francis, C. D. (2017). Natural and anthropogenic sounds reduce song performance: insights from two emberizid species. *Behav. Ecol.* 28, 974–982. doi: 10.1093/beheco/arx036

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., and Dooling, R. (2016). Communication masking in marine mammals: a review and research strategy. *Mar. Pollut. Bull.* 103, 15–38. doi: 10.1016/j.marpolbul.2015.12.007

Garamszegi, L. Z., and Moller, A. P. (2004). Extrapair paternity and the evolution of bird song. *Behav. Ecol.* 15, 508–519. doi: 10.1093/beheco/arh041

Gil, D., Honarmand, M., Pascual, J., Pérez-Mena, E., and Garcia, C. M. (2014). Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behav. Ecol.* 26, 435–443. doi: 10.1093/beheco/aru207

Gross, K., Pasinelli, G., and Kunc, H. P. (2010). Behavioral plasticity allows short-term adjustment to a novel environment. *Am. Nat.* 176, 456–464. doi: 10.1086/655428

Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., Ten Cate, C., et al. (2011a). Low-frequency songs lose their potency in noise urban conditions. *Proc. Natl. Acad. Sci. U.S.A.* 108, 14549–14554. doi: 10.1073/pnas.1109091108

Halfwerk, W., Holleman, L. J. M., and Slabbekoorn, H. (2011b). Negative impacts of traffic noise on avian reproductive success. *J. Appl. Ecol.* 48, 210–219. doi: 10.1111/j.1365-2664.2010.01914.x

Hamao, S., Watanabe, M., and Mori, Y. (2011). Urban noise and male density affect songs in the great tit *Parus major*. *Ethol. Ecol. Evol.* 23, 111–119. doi: 10.1080/03949370.2011.554881

Hanna, D., Blouin-Demers, G., Wilson, D. R., and Mennill, D. J. (2011). Anthropogenic noise affects song structure in red-winged blackbirds (*Agelaius phoeniceus*). *J. Exp. Biol.* 214, 3549–3556. doi: 10.1242/jeb.060194

Hill, S. D., Pawley, M. D., Anderson, M. G., and Ji, W. (2017). Higher song complexity and intruder pressure at dawn in a vocally complex songbird. *Emu* 118, 147–157. doi: 10.1080/01584197.2017.1380503

Hilty, S., and Christie, D. A. (2018). "Bananaquit (*Coereba flaveola*)," in *Handbook of the Birds of the World Alive*, eds J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana (Barcelona: Lynx Edicions).

Hoi-Leitner, M., Nechtelberger, H., and Hoi, H. (1995). Song rate as a signal for nest site quality in blackcaps (*Sylvia atricapilla*). *Behav. Ecol. Sociobiol.* 37, 399–405. doi: 10.1007/s002650050207

Huet des Aunay, G., Slabbekoorn, H., Nagle, L., Passas, F., Nicolas, P., and Draganoiu, T. I. (2014). Urban noise undermines female sexual preferences for low-frequency songs in domestic canaries. *Anim. Behav.* 87, 67–75. doi: 10.1016/j.anbehav.2013.10.010

Kagawa, H., and Soma, M. (2013). Song performance and elaboration as potential indicators of male quality in Java sparrows. *Behav. Processes* 99, 138–144. doi: 10.1016/j.beproc.2013.07.012

Kahle, D., and Wickham, H. (2013). ggmap: spatial visualization with ggplot2. *R J.* 5, 144–161. doi: 10.32614/rj-2013-014

Kaluza, B. F., Wallace, H., Heard, T. A., Klein, A. M., and Leonhardt, S. D. (2016). Urban gardens promote bee foraging over natural habitats and plantations. *Ecol. Evol.* 6, 1304–1316. doi: 10.1002/ece3.1941

Kipper, S., Mundry, R., Sommer, C., Hultsch, H., and Todt, D. (2006). Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. *Anim. Behav.* 71, 211–217. doi: 10.1016/j.anbehav.2005.04.011

Kleist, N. J., Guralnick, R. P., Cruz, A., and Francis, C. D. (2016). Anthropogenic noise weakens territorial response to intruder's songs. *Ecosphere* 7:e01259. doi: 10.1002/ecs2.1259

Kleist, N. J., Guralnick, R. P., Cruz, A., Lowry, C. A., and Francis, C. D. (2018). Chronic anthropogenic noise disrupts glucocorticoid signalling and has multiple effects on fitness in an avian community. *Proc. Natl. Acad. Sci. U.S.A.* 115, E648–E657. doi: 10.1073/pnas.1709200115

Lazerte, S. E., Slabbekoorn, H., and Otter, K. A. (2017). Territorial black-capped chickadee males respond faster to high-than to low-frequency songs in experimentally elevated noise conditions. *PeerJ* 5:e3257. doi: 10.7717/peerj.3257

Linhart, P., Slabbekoorn, H., and Fuchs, R. (2012). The communicative significance of song frequency and song length in territorial chiffchaffs. *Behav. Ecol.* 23, 1338–1347. doi: 10.1093/beheco/ars127

Lohr, B., Wright, T. F., and Dooling, R. J. (2003). Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Anim. Behav.* 65, 763–777. doi: 10.1006/anbe.2003.2093

Luther, D., and Magnotti, J. (2014). Can animals detect differences in vocalizations adjusted for anthropogenic noise? *Anim. Behav.* 92, 111–116. doi: 10.1016/j.anbehav.2014.03.033

Luther, D. A., Phillips, J., and Derryberry, E. P. (2016). Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. *Behav. Ecol.* 27, 332–340. doi: 10.1093/beheco/arv162

Mennitt, D. J., Fristrup, K. M., and Nelson, L. (2015). A spatially explicit estimate of environmental noise exposure in the contiguous United States. *J. Acoust. Soc. Am.* 137, 2339–2340. doi: 10.1121/1.4920539

Montague, M. J., Danek-Gontard, M., and Kunc, H. P. (2012). Phenotypic plasticity affects the response of a sexually selected trait to anthropogenic noise. *Behav. Ecol.* 24, 343–348. doi: 10.1093/beheco/ars169

Narango, D. L., and Rodewald, A. D. (2015). Urban-associated drivers of song variation along a rural-urban gradient. *Behav. Ecol.* 27, 608–616. doi: 10.1093/beheco/arv197

Nemeth, E., Zollinger, S. A., and Brumm, H. (2012). Effect sizes and the integrative understanding of urban bird song (A reply to Slabbekoorn et al.). *Am. Nat.* 180, 146–152. doi: 10.1086/665994

Parris, K. M., and McCarthy, M. A. (2013). Predicting the effect of urban noise on the active space of avian vocal signals. *Am. Nat.* 182, 452–464. doi: 10.1086/671906

Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* 51, 537–551. doi: 10.1111/j.1558-5646.1997.tb02441.x

Pohl, N. U., Leadbeater, E., Slabbekoorn, H., Klump, G. M., and Langemann, U. (2012). Great tits in urban noise benefit from high frequencies in song detection and discrimination. *Anim. Behav.* 83, 711–721. doi: 10.1016/j.anbehav.2011.12.019

Potvin, D., and MacDougall-Shackleton, S. A. (2015). Traffic noise affects embryo mortality and nestling growth rates in captive zebra finches. *J. Exp. Zool. A Ecol. Genet. Physiol.* 323, 722–730. doi: 10.1002/jez.1965

Potvin, D., and Parris, K. M. (2012). Song convergence in multiple urban populations of silvereyes (*Zosterops lateralis*). *Ecol. Evol.* 2, 1977–1984. doi: 10.1002/ece3.320

Potvin, D. A., and Mulder, R. A. (2013). Immediate, independent adjustment of call pitch and amplitude in response to varying background noise by silvereyes (*Zosterops lateralis*). *Behav. Ecol.* 24, 1363–1368. doi: 10.1093/beheco/art075

Quinn, J. L., Whittingham, M. J., Butler, J. S., and Cresswell, W. (2006). Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. *J. Avian Biol.* 37, 601–608. doi: 10.1111/j.2006.0908-8857.03781.x

R Core Team (2017). *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing.

Ríos-Chelén, A. A., Lee, G. C., and Patricelli, G. L. (2016). A comparison between two ways to measure minimum frequency and an experimental test of vocal plasticity in red-winged blackbirds in response to noise. *Behaviour* 153, 1445–1472. doi: 10.1163/1568539x-00003390

Ríos-Chelén, A. A., McDonald, A. N., Berger, A., Perry, A. C., Krakauer, A. H., and Patricelli, G. L. (2017). Do birds vocalize at higher pitch in noise, or is it a matter of measurement? *Behav. Ecol. Sociobiol.* 71:29. doi: 10.1007/s00265-016-2243-7

Ríos-Chelén, A. A., Quirós-Guerrero, E., Gil, D., and Garcia, C. (2013). Dealing with urban noise: vermilion flycatchers sing longer songs in noisier territories. *Behav. Ecol. Sociobiol.* 67, 145–152. doi: 10.1007/s00265-012-1434-0

Ripmeester, E. A. P., Mulder, M., and Slabbekoorn, H. (2010). Habitat-dependent acoustic divergence affects playback response in urban and forest population of the European blackbird. *Behav. Ecol.* 21, 876–883. doi: 10.1093/beheco/arq075

Shannon, C. E., and Weaver, W. (1949). *The Mathematical Theory of Communication*. Champaign, IL: University of Illinois Press.

Shochat, E. (2004). Credit or debit? Resource input changes population dynamics of city—slicker birds. *Oikos* 106, 622–626. doi: 10.1111/j.0030-1299.2004.13159.x

Slabbekoorn, H. (2012). "Measuring behavioural changes to assess anthropogenic noise impact on singing birds," in *Proceedings of Measuring Behavior*, eds A. J. Spink, F. Grieco, O. E. Krips, L. W. S. Loijens, L. P. J. J. Noldus, and P. H. Zimmerman (Utrecht: Noldus Information Technology), 28–31.

Slabbekoorn, H. (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* 85, 1089–1099. doi: 10.1016/j.anbehav.2013.01.021

Slabbekoorn, H., and Den Boer-Visser, A. (2006). Cities change the songs of birds. *Curr. Biol.* 16, 2326–2331. doi: 10.1016/j.cub.2006.10.008

Slabbekoorn, H., and Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature* 424, 267–267. doi: 10.1038/424267a

Slabbekoorn, H., and Ripmeester, E. A. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Mol. Ecol.* 17, 72–83. doi: 10.1111/j.1365-294x.2007.03487.x

Slabbekoorn, H., Yang, X. J., and Halfwerk, W. (2012). Birds and anthropogenic noise: singing higher may matter: (A comment on Nemeth and Brumm, "Birds and anthropogenic noise: are urban songs adaptive?"). *Am. Nat.* 180, 142–145. doi: 10.1086/665991

Soma, M., and Garamszegi, L. Z. (2011). Rethinking birdsong evolution: meta-analysis of the relationship between song complexity and reproductive success. *Behav. Ecol.* 22, 363–371. doi: 10.1093/beheco/arq219

Templeton, C. N., Zollinger, S. A., and Brumm, H. (2016). Traffic noise drowns out great tit alarm calls. *Curr. Biol.* 26, R1167–R1176.

Thompson, N. S., Ledoux, K., and Moody, K. (1994). A system for describing bird song units. *Bioacoustics* 5, 267–279. doi: 10.1080/09524622.1994.9753257

Tomiałojć, L. (1998). Breeding densities in some urban versus non-urban habitats: the Dijon case. *Acta Ornithol.* 33, 159–171.

Verzijden, M. N., Ripmeester, E. A. P., Ohms, V. R., Snelderwaard, P., and Slabbekoorn, H. (2010). Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. *J. Exp. Biol.* 213, 2575–2581. doi: 10.1242/jeb.038299

Wiley, R. H. (1994). "Errors, exaggeration, and deception in animal communication," in *Behavioral Mechanisms in Ecology*, ed. L. Real (Chicago, IL: University of Chicago Press), 157–189.

Winandy, G. S. M., Japyassú, H. F., Izar, P., and Slabbekoorn, H. (2021). Noise-related song variation affects communication: bananaquits adjust vocally to playback of elaborate or simple songs. *Front. Ecol. Evol.* 8:570431. doi: 10.3389/fevo.2020.570431

Wollerman, L., and Wiley, R. H. (2002). Background noise from a natural chorus alters female discrimination of male calls in a neotropical frog. *Anim. Behav.* 63, 15–22. doi: 10.1006/anbe.2001.1885

Wunderle, J. M. Jr., Cortes, R. A., and Carromero, W. (1992). Song characteristics and variation in a population of bananaquits on Puerto Rico. *Condor* 94, 680–691. doi: 10.2307/1369252

Zollinger, S. A., Podos, J., Nemeth, E., Goller, F., and Brumm, H. (2012). On the relationship between, and measurement of, amplitude and frequency in birdsong. *Anim. Behav.* 84, e1–e9. doi: 10.1016/j.anbehav.2012.04.026

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