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RECEIVED 12 January 2024

ACCEPTED 05 March 2024

PUBLISHED 03 April 2024

CITATION

Le Pogam A, O'Connor RS, Love OP, Young KG, Drolet J, Régimbald L, Roy G, Robitaille F, Berteaux D, Tam A and Vézina F (2024) Phenotypic constraints at the top of the world: an Arctic songbird faces the cumulative cost of maintaining a winter-like phenotype during breeding. *Front. Ecol. Evol.* 12:1369761. doi: 10.3389/fevo.2024.1369761

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Phenotypic constraints at the top of the world: an Arctic songbird faces the cumulative cost of maintaining a winter-like phenotype during breeding

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Among birds, several body composition traits typically decrease in size or mass during breeding likely as a result of competing demands during this critical life history stage. However, a recent outdoor captive study in an Arctic-breeding cold-specialist songbird (snow buntings – *Plectrophenax nivalis*) demonstrated that these birds maintain winter cold acclimatization during the spring and summer, despite facing summer temperatures much warmer than on their Arctic breeding grounds. This suggests that buntings may face a cumulative physiological cost during breeding: having to support a winter phenotype while also upregulating additional traits for reproduction. The current study aimed to test this hypothesis. Between 2016 and 2019, we examined how body composition and metabolic performance (thermogenic capacity and physiological maintenance costs) changed from pre-breeding to chick provisioning in free-living birds captured at the northern limit of their breeding range in the Canadian Arctic (Alert, NU, 82°). While body mass and fat reserves decreased significantly between pre-breeding and territory defense independent of thermal conditions, cold endurance and associated traits remained stable and elevated up to the nestling provisioning period, as long as ambient temperature remained below a threshold level of 0–2°C. These results indicate that snow buntings must maintain a high thermogenic capacity after arrival on the breeding grounds if temperatures remain below freezing, regardless of whether birds are actively breeding or not. In this context, our research suggests that these birds, and possibly other arctic breeding songbirds, may experience cumulative physiological costs during years with a late onset of spring, when breeding activities (i.e., egg production and incubation) begin while temperatures are still below 0–2°C.

KEYWORDS

Arctic birds, body composition, breeding, carry-over, cold acclimatization, life history stages, phenotypic flexibility, thermoregulation

1 Introduction

The annual cycle of migratory birds is composed of several life-history stages, including wintering, migratory and reproduction, which typically occur in a determined temporal sequence (Wingfield et al., 1999; Ramenofsky et al., 2003). However, in species experiencing short time windows for reproduction, such as those breeding at high latitudes or altitude, or those with irruptive breeding events, these life-history stages may also overlap in time (Hahn, 1995; Ramenofsky and Wingfield, 2006, 2017). For example, Arctic breeding birds often experience substantial snow accumulation, sub-zero temperatures and unpredictable weather upon arrival on their breeding grounds (e.g., Meltofte, 1983; Walsh et al., 2005; see also Morrison et al., 2007; Wingfield et al., 2011). Under such conditions, behavioral observations show that an overlap between winter and reproductive phenotypes may occur (Ramenofsky and Wingfield, 2006, 2017). Wingfield et al. (2004) have indeed reported winter behaviours, namely high sociability, hyperphagia and high mobility in white crowned sparrows (*Zonotrichia leucophrys gambelii*) facing harsh environmental conditions upon arrival on their breeding ground at Brook's Range (68°N), Alaska. These behaviours can be resumed later during the early stages of breeding if spring conditions deteriorate (Meltofte, 1983).

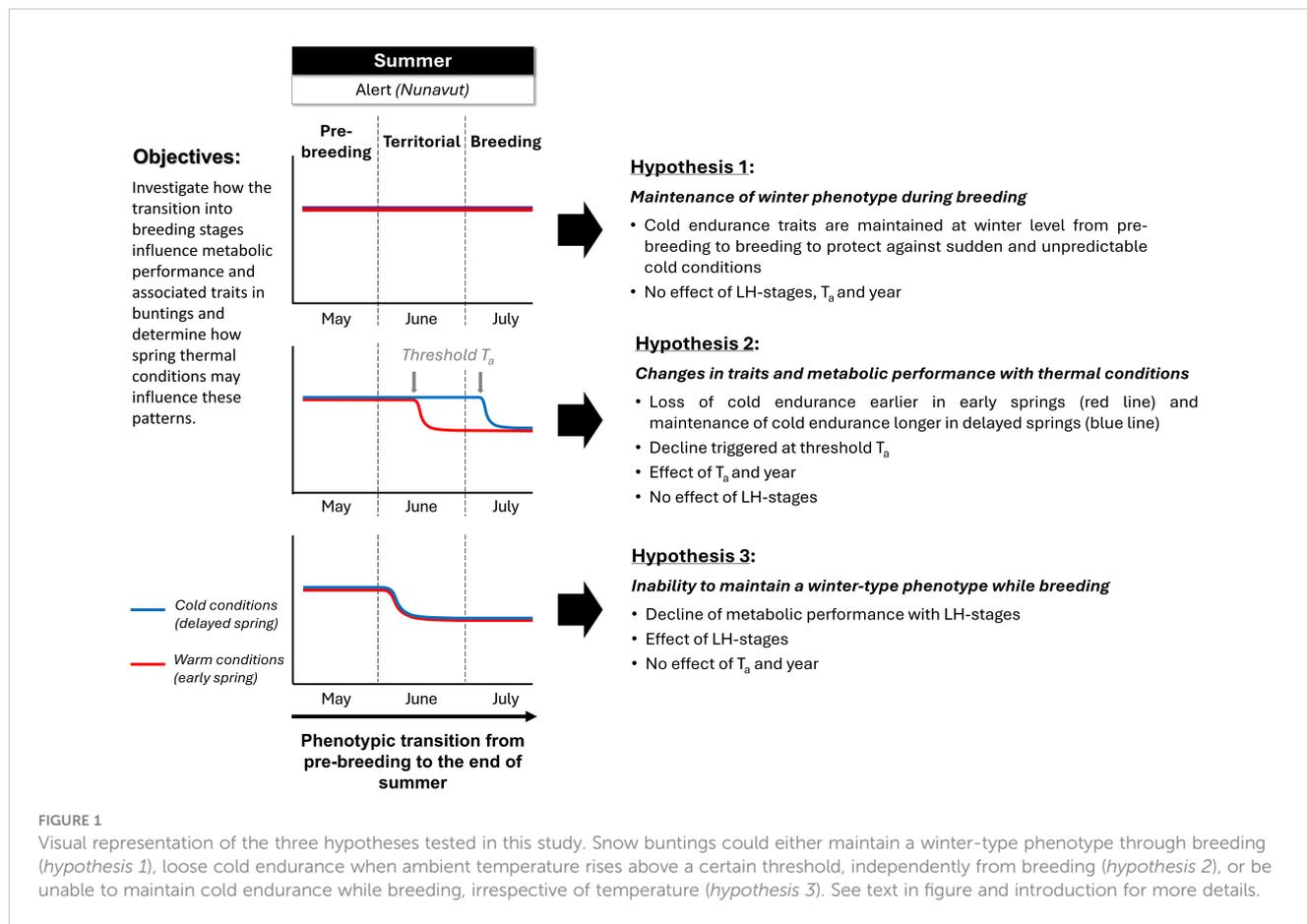
The occurrence of winter behaviors during the pre-breeding or breeding periods likely represents a way to cope with harsh or extreme conditions. However, other than endocrine regulation, which has received substantial attention (Wingfield et al., 2004; Ramenofsky et al., 2017; and see Ramenofsky and Wingfield, 2006 for a review) little is known about the underlying physiological adjustments implemented during these stage overlaps. In fact, taken separately, cold acclimatization and breeding involve significant morphological, physiological and metabolic changes to support energy demanding activities, which may or may not be compatible. For example, birds experiencing declines in ambient temperatures typically respond by increasing heart mass (Zheng et al., 2008; Petit and Vézina, 2014b), blood oxygen carrying capacity (hematocrit, Swanson, 1990b; O'Connor, 1996) and flight muscle size (O'Connor, 1995; Cooper, 2002; Swanson and Vézina, 2015; but see Barceló et al., 2017; Milbergue et al., 2018). Collectively these changes contribute to improving shivering heat production (Swanson, 1990b; Petit and Vézina, 2014a). In contrast, breeding birds typically lose both fat and muscle mass (Morrison et al., 2005; Morrison, 2006; Vézina et al., 2012), experience declines in oxygen carrying capacity (Morton, 1994; Morrison, 2006; Krause et al., 2016a) and develop large reproductive organs (Vézina and Salvante, 2010). At the moment, it is unclear to what degree these critical physiological transformations may overlap in time in support of breeding in cold environments such as the Arctic, especially considering that the timing of breeding can be closely tied to spring temperatures and snow cover (Høye et al., 2007; Moe et al., 2009; Grabowski et al., 2013).

Using captive snow buntings (*Plectrophenax nivalis*) as a model, Le Pogam et al. (2021b) recently showed that these Arctic cold specialists kept in outdoor aviaries on their wintering grounds (48°N) maintain thermogenic capacity and cold endurance comparable to the peak of winter over most of the summer, which corresponds to their breeding activities in the Arctic. In

other words, birds retained a cold acclimated phenotype during summer temperatures that greatly exceeded what is experienced on their Arctic breeding grounds [e.g., mean ambient temperature (T_a) in July and August: 20.3°C, range: 15.9–25.0°C]. This finding contrasts with previous studies showing ambient temperature as the main driver of thermogenic capacity in passerine birds (e.g., Saarela and Heldmaier, 1987; McKechnie and Swanson, 2010; Swanson, 2010). Le Pogam et al. (2021b) thus concluded that the maintenance of winter-like cold endurance throughout summer could provide further downstream advantages given that these birds can face unpredictable and snowy sub-zero conditions while breeding in the Arctic (Meltofte, 1983).

Although observations in captive snow buntings provide evidence for life-history overlap in Arctic breeders (Tinbergen, 1939; Meltofte, 1983; Wingfield and Hunt, 2002; Le Pogam et al., 2021b), the study by Le Pogam et al. (2021b) was nonetheless based on non-breeding, captive individuals. However, investment in a breeding phenotype typically involves considerable physiological changes including the loss of body mass and a reduction in oxygen carrying capacity and muscle mass, which combined could reduce cold endurance (O'Connor, 1995; Cooper, 2002; Dubois et al., 2016). Consequently, while we know that snow buntings maintain cold endurance at winter levels during spring migration and arrival (Le Pogam et al., 2021a), it is currently unclear whether, and if so, for how long, these birds can maintain this level of cold endurance while breeding. In addition, recent evidence has also shown that shivering heat production and cold endurance can vary independently from changes in muscle size (Stager et al., 2015; Milbergue et al., 2018; Le Pogam et al., 2020) or other physiological systems (Petit et al., 2013; Barceló et al., 2017). Therefore, patterns observed in captive birds could still reflect true endogenous cycles in buntings adapted to breed in cold, unpredictable Arctic environments (Le Pogam et al., 2021b).

Based on these recent discoveries, we sought to determine i) how the transition from a post-arrival cold-acclimated phenotype into a breeding phenotype (i.e., pre-breeding, territorial defense and nesting) influences metabolic performance and associated traits in snow buntings, and ii) how spring thermal conditions may influence these patterns. We formulated three hypotheses and related predictions to meet these two objectives. First (*Hypothesis 1*, Figure 1), snow buntings could maintain a winter-type phenotype for traits related to cold endurance into breeding to safeguard against unpredictable sudden cold conditions (Le Pogam et al., 2021b). In this case, we would expect birds to maintain traits (Table 1) at constant pre-breeding levels as they transition to territorial defense and breeding, independently from environmental conditions (i.e., temperature). Second (*Hypothesis 2*, Figure 1), cold endurance traits (Table 1) could mainly be driven by thermal conditions (Saarela and Heldmaier, 1987; McKechnie and Swanson, 2010; Swanson, 2010; Swanson et al., 2014), independently from breeding phenotypes. We would then expect performance traits to respond only to temperature, irrespective of the birds' breeding stages. In this scenario, as winter phenotypes appear to come with spare capacity, expressed as performance trait values plateauing below a certain ambient temperature (Petit and Vézina, 2014b; Swanson and Vézina, 2015; Vézina et al., 2020), one would expect snow buntings to lose cold endurance only when rising ambient temperature reaches a certain



threshold value. The birds would then undergo physiological changes and lose cold endurance rapidly in years with early springs, or maintain capacity longer when cold conditions last later into the season. The third hypothesis (*Hypothesis 3*, [Figure 1](#)) posits that snow buntings are unable to maintain a winter-type phenotype while breeding due to physiological changes in traits related to cold endurance ([Table 1](#)). In this specific case, one would therefore expect metabolic performance parameters to drop as birds transition from arrival into breeding, irrespective of spring temperatures. To test these three hypotheses, we examined inter-annual variation in phenotypic traits and metabolic performance in free-living buntings captured in the Canadian High Arctic during the pre-breeding stage (i.e., transition stage between arrival and dispersal onto breeding territories), during male territorial establishment, and during breeding, and then examined how temperature variation was associated with changes in phenotypic patterns.

2 Materials and methods

2.1 Study species

Snow buntings are an Arctic-breeding, migratory passerine known for their ability to endure cold environments ([Scholander et al., 1950a](#); [Le Pogam et al., 2020](#)). In the spring, birds migrate through cold winter landscapes ([McKinnon et al., 2016](#); [Snell et al., 2018](#)), with males

arriving on their breeding grounds to secure territories (up to 83.6°N) up to a month before females (March–April; [McKinnon et al., 2016](#); [Snell et al., 2018](#)). Ambient arrival conditions can be comparable or worse than those experienced at the peak of winter, with extensive snow cover and air temperatures (T_a) reaching -30°C ([Meltofte, 1983](#)). Buntings are known to arrive on the breeding grounds with winter level cold endurance ([Le Pogam et al., 2021a](#)) and can maintain winter-type behaviour for several weeks before dispersing to defend breeding territories ([Tinbergen, 1939](#); [Meltofte, 1983](#)).

2.2 Study sites, capture and measurements protocol

Snow buntings were studied in the Arctic during the springs of 2016 to 2019 at Alert, Nunavut, Canada ($82^{\circ}29'58''\text{N}$, $62^{\circ}28'5''\text{W}$). For this study, we distinguished three life-history stages (LH-stages): (1) the transition stage between arrival and dispersal onto breeding territories (hereafter pre-breeding, $n = 266$ birds), (2) the stage during which males sing and display to defend territories (hereafter territorial, $n = 66$ birds), and (3) the period during which males and females were paired (hereafter breeding). This last stage includes pair formation ($n = 11$), nest building ($n = 5$), egg laying ($n = 3$), incubation ($n = 6$), and nestling provisioning ($n = 21$). Sample sizes for each sub-stage were too small to consider them separately in analyses, and as such they were combined into one breeding stage category ($n = 46$).

TABLE 1 List of phenotypic traits measured in this study and their responses to cold and winter in passerine birds.

Metabolic performance			
Phenotypic traits	Interpreted as	Response to cold/winter	Pertinent references
Summit metabolic rate (M_{sum})	Maximum shivering thermogenic capacity, index of cold endurance	Typically higher	McKechnie and Swanson, 2010; Swanson, 2010; Petit et al., 2013; McKechnie et al., 2015; Le Pogam et al., 2020
Basal metabolic rate (BMR)	Maintenance energy expenditure, index of physiological maintenance costs	Often higher but not in snow buntings	McKechnie and Swanson, 2010; Swanson, 2010; Petit et al., 2013; McKechnie et al., 2015; <i>but see</i> Le Pogam et al., 2020
Phenotypic traits underlying metabolic performance			
Phenotypic traits	Interpreted as	Response to cold/winter	Pertinent references
Body mass	Total body composition	Typically higher	Carey et al., 1978; Liknes and Swanson, 1996; Zheng et al., 2008; Petit et al., 2014; Le Pogam et al., 2020
Fat store	Energy reserves	Typically higher	Blem, 1976; Lehikoinen, 1987; Gosler, 1996; Cooper, 2007; Le Pogam et al., 2020
Hematocrit	Blood oxygen carrying capacity	Typically higher	Swanson, 1990a; O'Connor, 1996; Le Pogam et al., 2020
Pectoralis muscle thickness	Shivering capacity	Typically increases with high metabolic rate	O'Connor, 1995; Cooper, 2002; Swanson and Merkord, 2012; Petit et al., 2013; Swanson and Vézina, 2015; Le Pogam et al., 2020

At the pre-breeding stage, birds were caught with walk-in or potter traps (Third Wheel, Devon, England) baited with commercial seed-mix (crushed corn, wheat, sorghum, white millet, red millet and black sunflower, Armstrong, Hagersville, ON, Canada). During the territorial and breeding stages, individuals were attracted to a double potter trap using song playback and a live male bunting as a decoy in one side of the trap. Birds were then captured on the other side of the trap or with spring traps (TWB45 Moudry, Říčany, Czech Republic) set close by.

Immediately after capture, a blood sample (<1% of M_b) was taken from the brachial vein. Blood samples were temporarily kept in cold storage and later centrifuged for 10 minutes at 8,000 RPM to obtain data on hematocrit (i.e., packed red blood cell volume). We then weighed ($\pm 0.01g$) and sexed birds according to the methods described in Smith (1992). We banded birds with a USGS numbered metal band as well as a unique combination of three darvic color bands to allow for identification from a distance. Morphometric measurements, namely length of head plus beak, tarsus, tail and right wing, were taken to calculate a “structural body size index” (see below). The size of fat stores was also estimated visually using a standard fat score index (from 0 = no visible fat in furculum area to 6 = fat overlapping pectoralis muscles, Love et al., 2012). The birds were then transferred to a field laboratory (less than 6km distance from capture site, transport time < 20 minutes) where we estimated pectoralis muscle thickness non-invasively by ultrasonography (Dietz et al., 1999; Wuenschel et al., 2006; Le Pogam et al., 2020) using a LOGIQe ultrasound scanner fitted with a linear probe (12MHz, GE Healthcare, Wauwatosa, WI, USA). Since the supracoracoideus muscle is very thin at the measured location, muscle thickness values essentially reflect thickness of the

pectoralis muscle. However, because ultrasound probe positioning can vary muscle thickness values, we also measured the height of the keel (see Le Pogam et al., 2020). Birds were then kept in cages (76cm W \times 46cm D \times 45cm H) with *ad libitum* water and seed (same mix as for captures) until metabolic performance measurements were complete (see below). In total, between 2016 and 2019, 311 males and 67 females were caught and banded during the breeding season (see Supplementary Table 1 for specific sample sizes).

2.3 Metabolic performance

For metabolic performance measurements, we used the set-up and protocol described in detail by Le Pogam et al. (2020, 2021b, 2021a), except that the oxygen analyzers used at Alert were two Sable Systems Foxboxes (Sable Systems, Las Vegas, NV, USA). Key points specific to this study are presented as follows.

Summit metabolic rate (M_{sum}) was measured on a maximum of two birds simultaneously, allowing up to two trials per day. Depending on the time of capture, measurements began between 08h50 and 22h45 (average: 14h45 \pm 2.89h; duration: 1h32 \pm 0.72h). Measurements took place at least one hour after ultrasound measurements. Birds were placed inside stainless steel metabolic chambers (effective volume 1.5L) and exposed to dry, CO₂-free air for 10 minutes at -18°C (or -9°C during the breeding stage) (flow rate of 1,200mL.min⁻¹), before switching to a helox gas mixture (21% oxygen, 79% helium, Rosenmann and Morrison, 1974). The chamber temperature was then lowered by 3°C every 20 minutes until birds became hypothermic (decline of $\dot{V}O_2$ for several minutes and body temperature $\leq 37^\circ\text{C}$, Swanson and Liknes, 2006) or

reached the end of the preprogrammed trial. Six measurements out of 85 (7%) involved birds that were not hypothermic by the end of the trial. However, since hypothermia is not a prerequisite to confirm M_{sum} (Dutenhoffer and Swanson, 1996), we opted to include these individuals in final analyses. Removing them had no influence on results.

We measured basal metabolic rates (BMR) overnight on a maximum of four birds simultaneously. The BMR trials began between 18h25 and 1h26 (average start time: 19h38 \pm 5.07h). We insured a minimum 1h of rest after the M_{sum} measurements. Using the same metabolic chambers as for M_{sum} , birds were exposed to 25°C, a temperature within the snow bunting thermoneutral zone (Scholander et al., 1950b) and received dry CO₂-free air (flow rate of 650 mL.min⁻¹) for the duration of trials (12h49 \pm 5.9h on average). Birds were weighed (\pm 0.01 g) before and after measurements, and average M_b was used in BMR analyses. We used a sampling frequency of 5 secs for M_{sum} and 20 secs for BMR. Both M_{sum} and BMR were calculated from the highest and lowest averaged 10 min trace of $\dot{V}O_2$, respectively, using equation 10.1 from Lighton (2019), using the instantaneous measurement technique (Bartholomew et al., 1981) for M_{sum} . The duration of BMR trials ensured that birds were post-absorptive at the time of BMR measurement. We estimated energy expenditure for all metabolic measurements using a constant equivalent of 19.8kJ L⁻¹O₂ and converted units to Watts (Gessaman and Nagy, 1988).

2.4 Weather data

Weather data were obtained from the Environment and Climate Change Canada Alert weather station (i.e., our study site). More specifically, we extracted daily data for T_a mean and produced 7-day averages that were then used in statistical analyses.

2.5 Statistical analysis

Analyses proceeded in two steps. First, we used general linear models with M_b , fat score, hematocrit, pectoralis muscle thickness, M_{sum} and BMR as separate response variables. All models included year, LH-stage (i.e., pre-breeding, territorial and breeding), mean ambient temperature (hereafter T_a) and their interactions as predictor variables. We chose to use 7-day mean temperature (6 days prior to capture + day of capture) because earlier reports showed that metabolic performance responds to relatively short term variation in temperature (short and medium term variation as presented by Swanson and Olmstead, 1999). We also added time of day at capture (for M_b and fat score), structural size (for M_b), keel height (for pectoralis muscle thickness) and M_b and length of captivity (for M_{sum} and BMR) as covariates in models. Since several structural size parameters were collected for the same individual, the estimate of “structural body size” was based on the first component obtained from a principal component analysis combining variation in the lengths of head plus beak, wing and tail (Rising and Somers, 1989). Since females do not have a “territorial” stage (only males defend territories; Tinbergen, 1939), the variable “sex” was not include in these models.

In the second step, we further analyzed how pectoralis muscle thickness, hematocrit and mass-independent M_{sum} varied with T_a in interaction with LH-stage and/or year. These variables were the only ones where significant interactions were found (see Results). Linear regression analyses were therefore performed per year and/or per LH-stage. We used piecewise linear regression models to determine whether response variables declined at a given threshold T_a . In this set of analyses, we used the residuals of M_{sum} corrected for body mass (hereafter residual M_{sum}) and residuals of pectoralis muscle thickness corrected for keel height (hereafter residual pectoralis muscle thickness). Visual inspection of residuals confirmed assumptions of normality and homogeneity for all models. All analyses were conducted using JMP pro (14.0.0) and data are presented as mean \pm standard error of the mean (s.e.m.). Effects were considered significant and retained in models when $P < 0.05$.

3 Results

3.1 Weather conditions

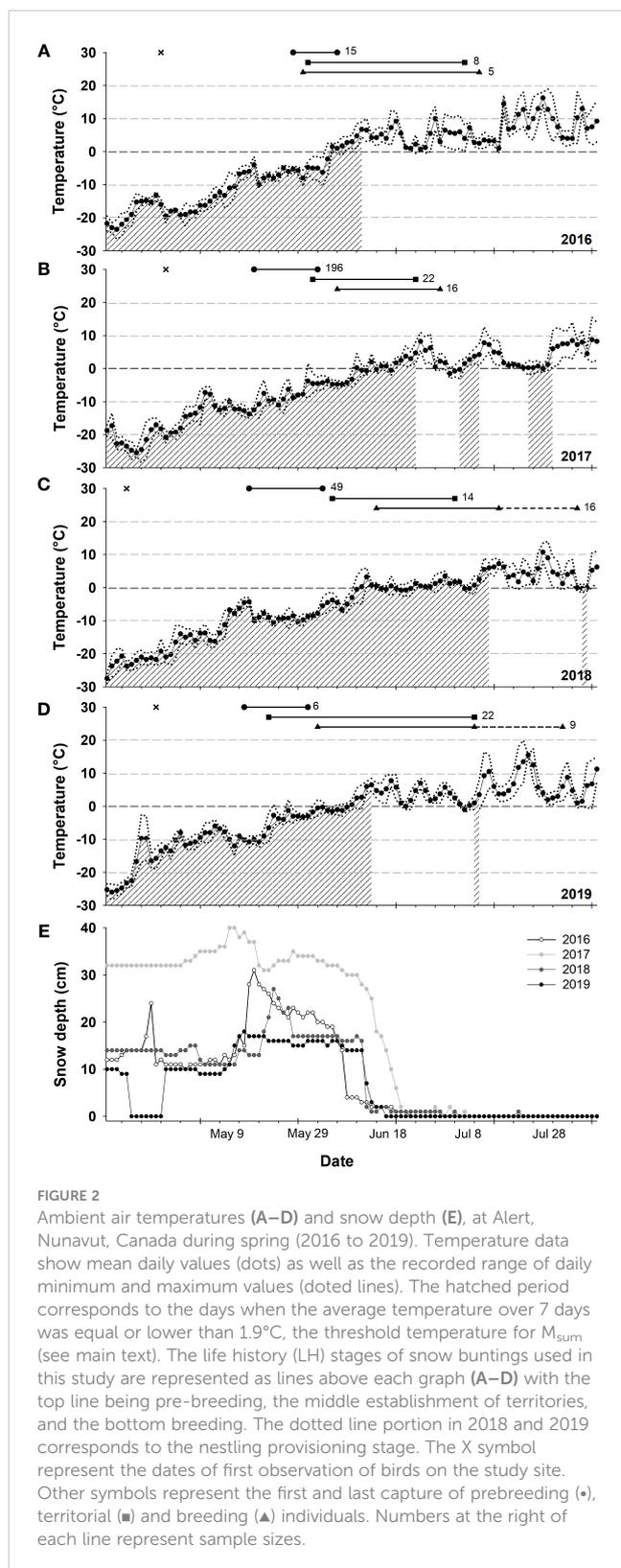
At Alert, daily mean T_a exceeded 0°C at the earliest on June 2 in 2019 and at the latest on June 11 in 2018 (Figure 2). The years 2016 and 2019 had the fastest temperature increases (Figure 2, Table 2). However, there was more snow on the ground and rapid snow melt occurred up to 10 days later in 2017 than in other years (Figure 2).

3.2 Effects of LH-stage and T_a on metabolic performance and associated traits

Controlling for the effect of time at capture and body size, M_b was significantly affected by LH-stage, but not by T_a or year (Table 3). M_b was 14.4% higher during pre-breeding than during territorial defense (Tukey’s HSD $P < 0.0001$) and M_b at that latter stage did not differ from that measured during breeding (pre-breeding vs breeding: Tukey’s HSD $P < 0.0001$, Figure 3A). Fat score followed a similar pattern (Table 3), with birds carrying less fat during territorial defense (pre-breeding vs territorial: Tukey’s HSD $P < 0.0001$) and during breeding (pre-breeding vs breeding: Tukey’s HSD $P < 0.005$) than at pre-breeding (Figure 3B).

The influence of temperature on hematocrit was dependent on both LH-stage and year (see interaction terms in Table 3). Regressions performed within LH-stages showed that hematocrit decreased as T_a increased, but only during breeding (Figure 4). However, piecewise linear regression combining all data showed no inflection point for hematocrit.

Pectoralis muscle thickness varied among both years and LH-stages (Table 3). However, these effects occurred in interaction with T_a (see interaction terms in Table 3). Regression analyses per LH-stages revealed that residual pectoralis muscle thickness decreased with warming T_a only during breeding (Figure 5). Regressions per year showed a significant negative relationship between residual pectoralis muscle thickness and T_a , but only in 2017 (Figure 5). Piecewise regression combining all data revealed an inflection point



at $0.1 \pm 1.6^\circ\text{C}$ (Figure 6A). Above that temperature, residual pectoralis muscle thickness declined with increasing T_a (Figure 6A).

Summit metabolic rate, whether considered whole (not shown) or corrected for M_b , differed among years and LH-stages, but both these effects depended on T_a (interaction terms in Table 3). As with hematocrit and pectoralis muscle thickness, regressions within LH-

stages showed a negative linear relationship between residual M_{sum} and T_a only during breeding (Figure 7). Intra-annual regression analyses also showed a negative relationship between residual M_{sum} and T_a , but only in 2019 (Figure 7). Piecewise regression performed on all data highlighted an inflection point at $1.9 \pm 2.6^\circ\text{C}$ (Figure 6B). Above that temperature, residual M_{sum} declined with warming temperature (Figure 6B).

Whole basal metabolic rate varied with LH-stage ($F_{2,146} = 21.7$, $P < 0.001$, not shown), but this effect was driven by the loss of M_b among stages (Figure 3). Considering the significant influence of M_b (in addition to that of length of captivity), we found no significant influence of year, T_a or LH-stage on BMR (Table 3). Maintenance costs remained constant at $0.56 \pm 0.01\text{W}$ from spring to end of summer.

4 Discussion

The objective of this study was to examine whether metabolic performance and associated traits in snow buntings remained at post-arrival level (i.e., winter level; Le Pogam et al., 2021a) across three Life History (LH) stages on their breeding grounds, or whether performance declined in response to temperature and/or breeding stages. Overall, although all traits did not show the same pattern, our results suggest that in snow buntings, thermogenic capacity declines during active breeding, but only if ambient temperatures rise above freezing.

4.1 Body mass and fat storage decline as birds begin to breed

After considering the effects of structural body size and time at capture, both body mass and fat scores were only affected by life history stages in snow buntings. Indeed, mass and fat scores both declined from pre-breeding to the territorial stage and then remained low thereafter during breeding. As this finding was independent from the effects of temperature and year, these results support the idea that birds could not maintain mass and energy stores at winter levels while breeding (Hypothesis 3, Figure 1).

A decline in body mass and fat stores during the establishment of breeding territories is common in passerines (e.g., Ramenofsky and Wingfield, 2006; Krause et al., 2016b). For species breeding at high latitudes, this phenomenon generally coincides with the dispersal of post-arrival flocks and the secretion of reproductive hormones (see Ramenofsky and Wingfield, 2006 for a review). Snow buntings also become very active as they initiate breeding activities. For example, the period of territorial defense is characterized by high rates of singing in males, courtship displays where the birds climb in altitude and sing while gliding down as well as physical fights between competing males (Romero et al., 1998; Guindre-Parker et al., 2013). Once breeding pairs have formed, males and females are highly mobile during nest building and both adults maintain high rates of nestling provisioning after the eggs have hatched (Tinbergen, 1939; Lyon et al., 1987), with daily resting

TABLE 2 Average monthly ambient air temperatures during the breeding season recorded at Alert (NU) between 2016 and 2019.

Ambient air temperature T_a (°C) at Alert				
Mean T_a per year (Alert)	2016	2017	2018	2019
April	-24.5 ± 6.3 ^a	-22.5 ± 3.3 ^a	-24.7 ± 2.7 ^a	-22.7 ± 5.0 ^a
May	-11.4 ± 5.3 ^a	-11.8 ± 4.1 ^a	-11.7 ± 4.4 ^a	-8.1 ± 3.6 ^b
June	3.1 ± 3.9 ^a	0.03 ± 3.6 ^b	-1.2 ± 3.2 ^b	2.6 ± 2.9 ^a
July	8.1 ± 4.3 ^a	4.2 ± 3.1 ^b	3.9 ± 2.9 ^b	6.1 ± 4.5 ^{ab}

Letters indicate significant differences (Tukey’s HSD $P < 0.05$) between years within months.

periods typically being limited to 3–5h per day (Hussell, 1972). In fact, nestling growth rates in snow buntings are among the highest in passerines of that body size (i.e., 11.5–13% of adult body weight gain per day; Hussell, 1972), with only 8–10 days from hatching to

fledging, with nestlings unable to fly at fledging (Hussell, 1972). With the high energy cost of flapping flight in birds (Hedenstrom, 1993) and the busy schedule of breeding snow buntings, it may simply not be possible for these birds to maintain body mass and fat

TABLE 3 Linear effects models comparing phenotypic traits among life-history stages in snow buntings breeding at Alert, Nunavut, Canada.

Variable	Body mass			Fat score		
	df	F	P	df	F	P
T_a mean	1, 357	0.0035	0.95	1, 364	0.21	0.65
Year	3, 355	0.21	0.89	3, 362	0.21	0.89
LH-stage	2, 356	28.95	<0.0001	2, 363	18.74	<0.0001
LH-stage x Year	-	-	-	-	-	-
LH-stage x T_a mean	-	-	-	-	-	-
Year x T_a mean	-	-	-	-	-	-
Year x LH-stage x T_a mean	-	-	-	-	-	-
Time at capture	1, 357	5.36	0.02	1, 364	3.41	0.07
Structural size	1, 357	40.68	<0.0001	NA	NA	NA
Variable	Hematocrit			Pectoralis muscle thickness		
	df	F	P	df	F	P
T_a mean	1, 232	4.06	0.05	1, 185	0.63	0.43
Year	3, 230	1.62	0.18	3, 183	4.38	0.005
LH-stage	2, 231	1.47	0.23	2, 184	4.54	0.01
LH-stage x Year	6, 227	3.71	0.002	-	-	-
LH-stage x T_a mean	2, 231	0.84	0.43	2, 184	11.08	<0.0001
Year x T_a mean	3, 230	1.96	0.12	3, 183	4.24	0.006
Year x LH-stage x T_a mean	6, 227	2.20	0.04	-	-	-
Keel height	NA	NA	NA	1, 185	276.09	<0.0001
Variable	Mass-independent M_{sum}			Mass-independent BMR		
	df	F	P	df	F	P
T_a mean	1, 72	1.83	0.18	1, 146	0.07	0.80
Year	2, 71	7.42	0.001	3, 144	0.85	0.47
LH-stage	2, 71	2.56	0.08	2, 145	0.54	0.58
LH-stage x Year	-	-	-	-	-	-

(Continued)

TABLE 3 Continued

Variable	Mass-independent M_{sum}			Mass-independent BMR		
	df	F	P	df	F	P
LH-stage x T_a mean	2, 71	3.95	0.02	-	-	-
Year x T_a mean	2, 71	3.37	0.04	-	-	-
Year x LH-stage x T_a mean	-	-	-	-	-	-
Mass	1, 72	7.98	0.006	1, 146	56.41	<0.0001
Length of captivity	NA	NA	NA	1, 146	8.51	0.004

Models also included covariates meaningful to specific dependent variables. See text for details. Values in bold indicate p-value of 0.05 or lower. Covariables marked NA mean that they are not included in the model.

stores at winter levels, even if thermal conditions can be highly unpredictable in the Arctic (Table 2). Alternatively, but not exclusively, maintaining a lower body mass at these stages could also be adaptive as it reduces flight costs during a period of high energy demand (Merkle and Barclay, 1996; Nagy et al., 2007; Boyle et al., 2012).

While the variation in body mass and fat stores reported here is consistent with that of other free-living species, it contrasts with previous observations in captive snow buntings (Navarro and Gutiérrez, 1995; Le Pogam et al., 2021b). Both Navarro and Gutiérrez (1995) and Le Pogam et al. (2021b) observed that when maintained at their wintering latitude throughout summer, this species maintains body mass and fat stores above their winter average until at least the end of June. Similar observations have also been made in other captive migrant species (Eyster, 1954;

Gwinner and Czeschlik, 1978; Schwabl and Farner, 1989), which have led others to hypothesize that different endocrine responses, lack of visual cues or reproductive opportunities in captivity (Gwinner and Czeschlik, 1978; Schwabl and Farner, 1989) could trigger this effect. Although this is possible, captive studies have also shown strong endogenous regulation of seasonal cycles in migrant species (Ramenofsky and Wingfield, 2006; Vézina et al., 2011; Karagicheva et al., 2016). It could therefore also be that snow buntings are pre-programmed, via their endogenous circannual cycle, to maintain high energy intake rates during breeding as this occurs at a time of very high daily energy expenditure (Vézina et al., 2011; Karagicheva et al., 2016). In free-living breeding conditions, this would be enough to balance energy budgets and maintain stable (but lower) body mass, while in captivity maintaining high intake rates in birds not able to breed could lead to fat stores and body mass comparable to or above wintering levels.

4.2 Maintenance costs decline with breeding, but cold endurance traits respond to warming temperatures

Basal metabolic rate is interpreted as a measure of physiological maintenance costs and is thought to reflect changes in the activity and amount of tissues forming an animal (Piersma and Lindström, 1997; Piersma et al., 2004; Swanson et al., 2017a). We found that total maintenance costs declined as birds lost body mass with territorial defense and breeding, but that tissue metabolic intensity (mass corrected BMR) remained constant. We also found that these patterns were independent of variation in ambient temperature. Since territorial defense and nestling provisioning are energetically demanding activities for snow buntings, lower overall maintenance costs could be beneficial to balance energy budgets at that time (Swanson et al., 2017b). This finding contrasts with an earlier report of increasing BMR in shorebirds breeding at Alert (Vézina et al., 2012), although a large portion of this variation was attributed to migration recovery in recently arrived birds. Female birds have also been shown to have higher BMR during egg development (Chappell et al., 1999; Salvante et al., 2010; Vézina and Salvante, 2010). However, our data did not include measurements at that stage.

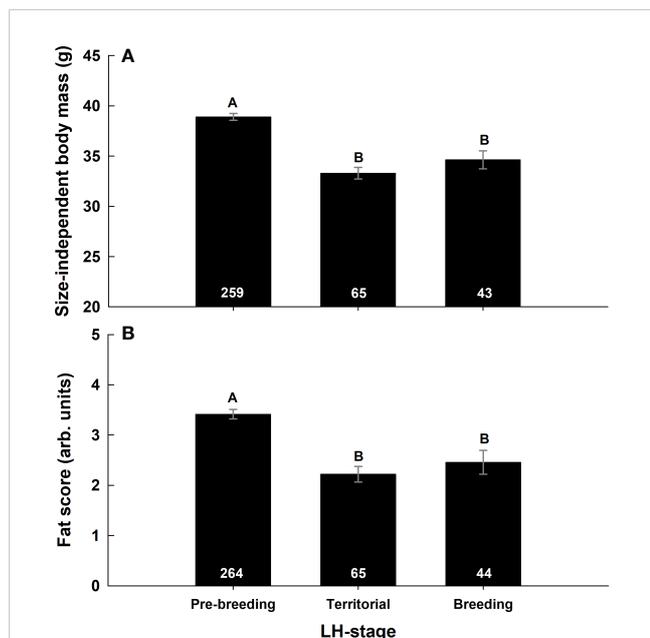


FIGURE 3 The effect of life history (LH) stage on size-independent body mass (A) and fat score (B) in snow buntings breeding at Alert, Nunavut, Canada. Letters indicate significant differences (Tukey's HSD $P < 0.05$). Numbers within bars indicate sample size for each group. Values presented as mean \pm SEM.

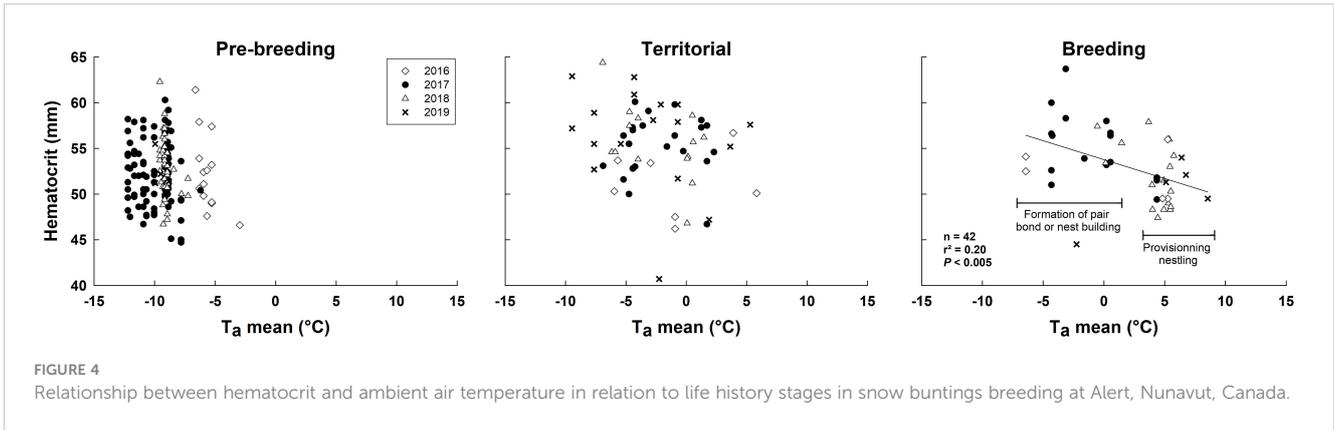


FIGURE 4 Relationship between hematocrit and ambient air temperature in relation to life history stages in snow buntings breeding at Alert, Nunavut, Canada.

Our data on hematocrit, pectoralis muscle thickness and M_{sum} showed comparable patterns regarding life-history stages and ambient temperature. Values for all three variables remained relatively stable during the pre-breeding and territorial stages, but declined with warming temperatures during breeding. In other words, warming temperature led to a loss of cold endurance as predicted under *Hypothesis 2*, but only when the birds were actively breeding, also providing support for *Hypothesis 3*. In fact, although sample size limitations prevented us from testing for within-breeding-stage effects (e.g., nest building, incubation and provisioning) *Figures 4–7* indicate that the temperature-related decline in these traits appears to occur during the highly active period of nestling provisioning. However, this stage also coincides with temperatures above 0°C in all years. Results further suggest that in some years temperature may also act on muscle size (in 2017, *Figure 5*) and M_{sum} (in 2019, *Figure 7*) independently from life-history stage. Although the overlap in time makes the independent influence of temperature and breeding stages difficult to tease apart, several lines of evidence, together with previous studies, lead us to posit that variation in ambient temperature, rather than the direct effects of breeding, is the main driver of the observed decline in cold endurance in breeding snow buntings.

We observed a decline in pectoralis muscle thickness as temperature increased during breeding, with the lowest values recorded in birds provisioning nestlings. It is possible that the high locomotor activity required during foraging and provisioning led to muscle loss, as is often observed in other species during migration (e.g., *Battley et al., 2000; Bauchinger et al., 2005*), and to a correlated decline in M_{sum} since shivering heat production covaries with muscle size in buntings (*Dubois et al., 2016; Le Pogam et al., 2020; Le Pogam et al., 2021b*). However, migration-related muscle loss results from unbalanced protein turnover due to a negative energy budget during flights (i.e., no or little replacement for degraded proteins as birds lose mass; *Bauchinger and McWilliams, 2010, 2010*; but see *Gerson and Guglielmo, 2011*). In our study, buntings did not show signs of negative energy balance once territorial defense had been initiated. In fact, both body mass and fat scores remained stable between territorial and breeding stages (*Figure 3*). Furthermore, experimental studies have shown that exercise in birds leads to an increase in pectoralis muscle mass and not a decrease as we observed here (*Zhang et al., 2015, 2018*). Additionally, seasonal declines in muscle mass and M_{sum} have been observed at the end of winter as temperatures warm up in non-migrant species coming out of cold wintering conditions (e.g., *Petit*

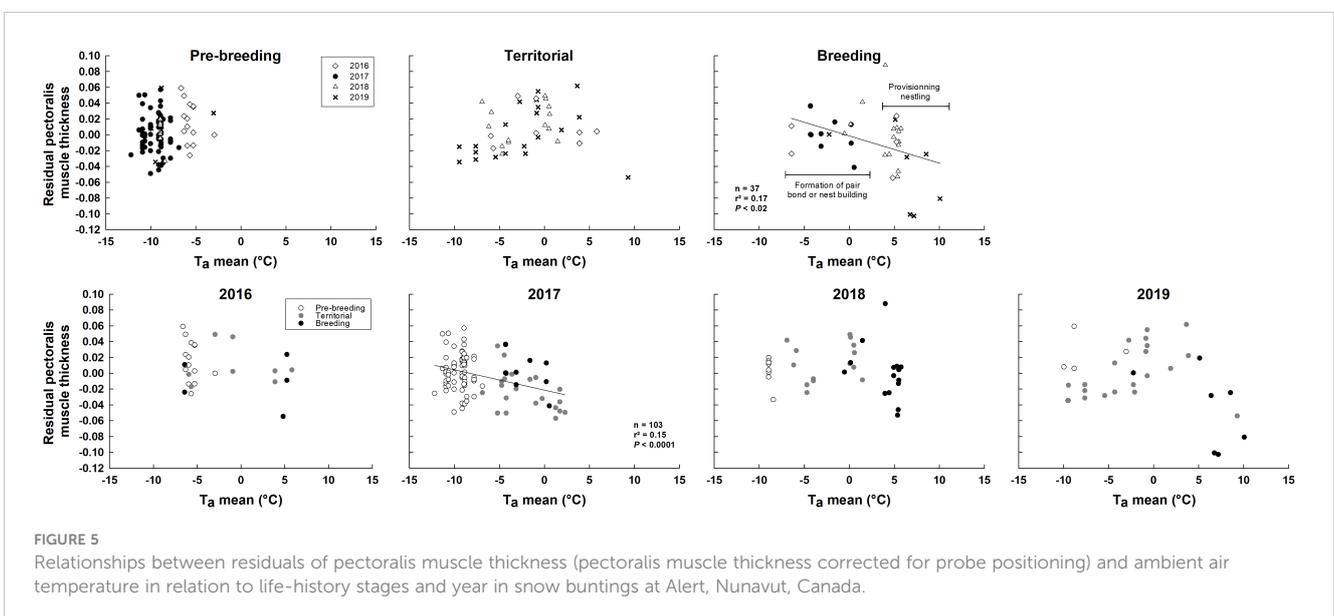


FIGURE 5 Relationships between residuals of pectoralis muscle thickness (pectoralis muscle thickness corrected for probe positioning) and ambient air temperature in relation to life-history stages and year in snow buntings at Alert, Nunavut, Canada.

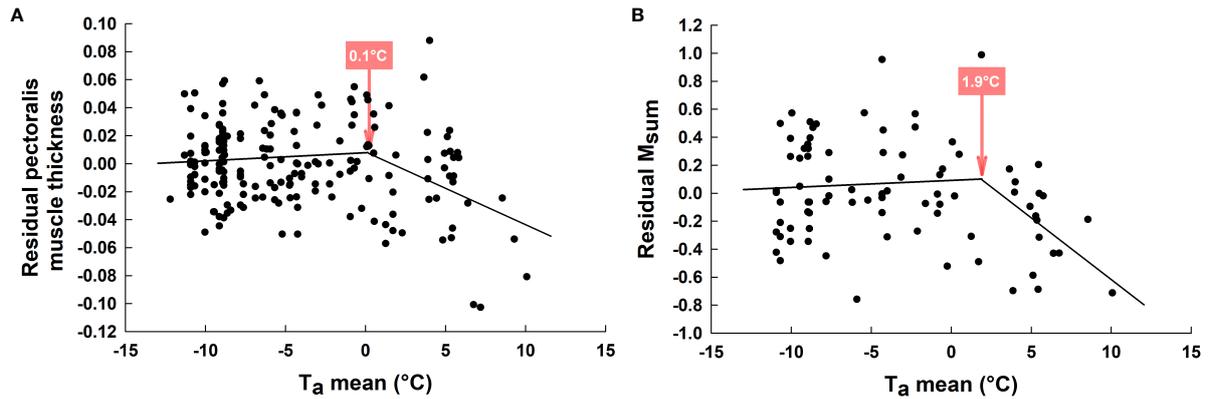


FIGURE 6
 Relationship between residuals of muscle thickness (pectoralis muscle thickness corrected for probe positioning) and ambient temperature (A) and between residuals of M_{sum} (M_{sum} corrected for body mass) and ambient air temperature (B) in snow buntings at Alert, Nunavut, Canada. Temperature values and arrows show the inflexion points for these two parameters.

et al., 2014). Such a pattern has also been observed in outdoor captive snow buntings exposed to summer temperatures on their wintering grounds (Le Pogam et al., 2021b). Indeed, although Le Pogam et al. (2021b) did not test for an influence of temperature on muscle thickness per se, they nonetheless reported muscle sizes comparable to winter in March and April (corresponding to migration), and a relatively slow, but constant, decline through the rest of summer that was paralleled by a reduction in M_{sum} . Therefore, as these captive birds could not breed, we believe that changes in muscle size in breeding buntings, combined with the parallel changes in M_{sum} , are more likely to result from rapidly improving thermal conditions than from a consequence of the birds' breeding activity.

We also found a negative relationship between hematocrit level and ambient temperature, but only during breeding when thermal conditions had improved. Breeding related changes in avian

hematocrit have been reported before (Morton, 1994; Fair et al., 2007; Krause et al., 2016a). For example, female birds typically experience hematocrit declines prior to egg-laying due to an increase in plasma estrogen inhibiting erythrocyte synthesis (Wagner et al., 2008; Williams et al., 2012), but this effect disappears during active nestling provisioning, the period matching the decline observed in this study (Morton, 1994; Williams et al., 2004; Krause et al., 2016a and see Fair et al., 2007 for a review). In males, however, hematocrit is positively related to testosterone (Buttemer and Astheimer, 2000) and testosterone does decline when males begin to provision nestlings in buntings (Romero et al., 1998). Nevertheless, although hematocrit typically increases with exercise (Bairlein and Totzke, 1992; Morton, 1994; Piersma et al., 1996), it has consistently been found to correlate negatively with ambient temperature in birds (DeGraw et al., 1979; Rehder and Bird, 1983; Fair et al., 2007). This marker of oxygen

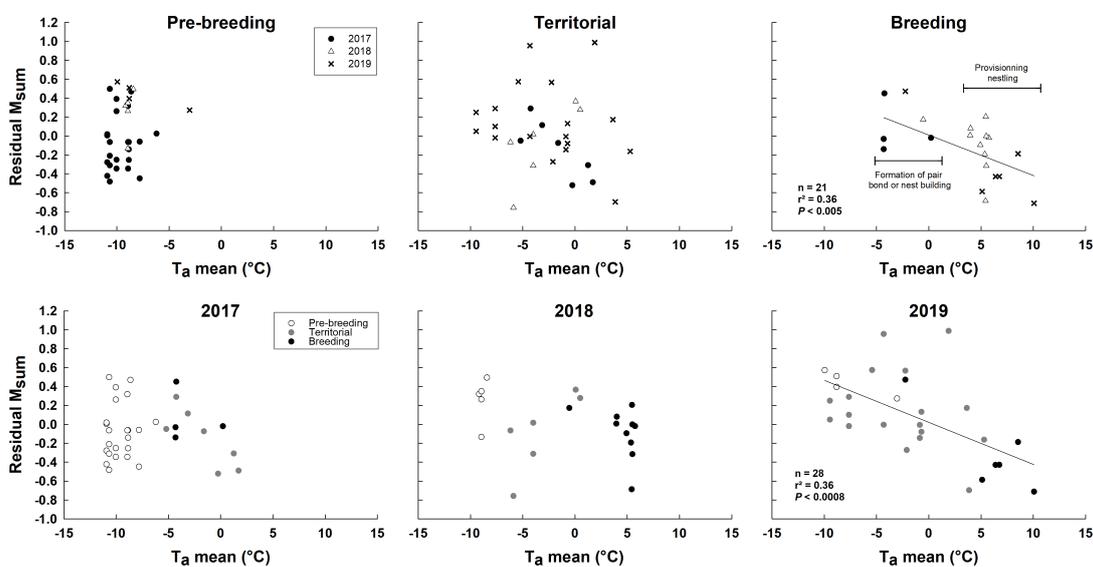


FIGURE 7
 Relationship between residuals of M_{sum} (M_{sum} corrected for body mass) and ambient air temperature according to life-history stages and year in snow buntings at Alert, Nunavut, Canada.

carrying capacity is also directly and positively correlated with thermogenic capacity (Swanson, 1990a; Petit and Vézina, 2014a), including in snow buntings (Le Pogam et al., 2020; Le Pogam et al., 2021b). It is therefore likely that the hematocrit reduction observed in breeding buntings results from increasingly favorable thermal conditions. As blood oxygen carrying capacity and cardiac function appears to support maximal shivering heat production (Petit et al., 2014; Vézina et al., 2017) this effect probably underlies part of the observed temperature dependent changes in M_{sum} .

4.3 Snow buntings may be paying cumulative physiological costs in late spring years

Our observations suggest that variation in oxygen carrying capacity, muscle size and M_{sum} may be more strongly influenced by warming summer temperatures than by breeding activities in snow buntings. These findings support results from several studies on avian cold endurance published since the 1990s showing the proximate influence of temperature on thermogenic capacity (Swanson and Olmstead, 1999; McKechnie and Swanson, 2010; Swanson, 2010 for reviews). In fact, combining data across years and breeding stages (Figure 6), we observed that pectoralis muscle thickness began declining once ambient temperatures warmed above 0°C. Thermogenic capacity followed closely and began to decline at temperatures above 2°C (Figure 6). Therefore, our results for traits underlying cold endurance are consistent with the M_{sum} reaction norm reported in other birds (Petit and Vézina, 2014b; Swanson and Vézina, 2015) and support the hypothesis that snow buntings maintain thermogenic capacity after their arrival if temperatures remain below freezing, whether they are actively breeding or not (Hypothesis 2, Figure 1).

This finding of a threshold temperature effect on the maintenance of thermogenic capacity is important because it suggests that snow buntings likely incur cumulative physiological costs in years with a late onset of spring where breeding activities may begin at temperatures well below 0–2°C. The timing of our own data collection confirms this idea (see Figure 2). While nestling provisioning clearly occurs at temperatures above freezing, other important stages such as egg production and incubation may begin (2016, 2019) or occur almost completely (2017, 2018) at temperatures requiring the maintenance of winter levels of thermogenic capacity and cold endurance. Other species, such as the Canada jay (*Perisoreus canadensis*) are known to initiate breeding at sub-zero temperatures (e.g., –10°C); however, these birds are larger than snow buntings and rely on considerable amounts of cached food to support their energy requirements (Whelan et al., 2016). Experimental studies with birds breeding in the cold have shown reduced rates of egg production, delayed laying and smaller clutches (Salvante et al., 2007), as well as reduced locomotor activity and potential energy reallocation among physiological systems when birds must combine cold acclimation and breeding (Salvante et al., 2010). The extent to which maintaining winter level cold endurance in late Arctic springs

may or may not be restrictive in actively breeding snow buntings will therefore require more research.

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 approved by the animal care committee of the Université du Québec à Rimouski (CPA-61-15-163 and CPA-71-17-194) and was conducted under scientific (SC-48) and banding (10889E) permits from Environment and Climate Change Canada. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

ALP: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. RO: Writing – original draft, Writing – review & editing. OL: Funding acquisition, Resources, Supervision, Writing – original draft, Writing – review & editing. KY: Data curation, Investigation, Writing – review & editing. JD: Data curation, Investigation, Writing – review & editing. LR: Data curation, Investigation, Writing – review & editing. GR: Data curation, Investigation, Writing – review & editing. FR: Data curation, Investigation, Writing – review & editing. DB: Resources, Writing – review & editing. AT: Funding acquisition, Resources, Writing – review & editing. FV: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This research benefited from a generous donation from the Kenneth M. Molson Foundation. It was also supported by NSERC Discovery grants to FV and OL, Canada Foundation for Innovation (CFI) awards to FV and OL, Canada Research Chair funding to OL, as well as logistical support and funding from the Department of National Defense to FV and DB.

Acknowledgments

We thank François Fournier from Environment and Climate Change Canada for help with logistical support in the initial Alert phase of this project. We thank Jonathan Coude for technical support and Alain Caron for statistical advice. We thank Chris

McRae and Nathan Koutroulides for help with logistics and the personnel from CFS Alert for their support during fieldwork. We are grateful to the field team for their punctual help in 2019: Emilie Desjardins, Sandra Lai, Marie-Pierre Poulin, Marie-Jeanne Rioux and Jacob Caron Carrier. We thank the reviewers for their constructive comments on the earlier versions of this article. This research is part of the PhD thesis of A. Le Pogam at Université du Québec à Rimouski (Le Pogam, 2021).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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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.2024.1369761/full#supplementary-material>

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