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Born in the cold: contrasted thermal exchanges and maintenance costs in juvenile and adult snow buntings on their breeding and wintering grounds

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Abstract

Several species of passerines leave their nest with unfinished feather growth, resulting in lower feather insulation and increased thermoregulatory demands compared to adults. However, feather insulation is essential for avian species breeding at northern latitudes, where cold conditions or even snowstorms can occur during the breeding season. In altricial arctic species, increased heat loss caused by poor feather insulation during growth could be counter-adaptive as it creates additional energy demands for thermoregulation. Using flow-through respirometry, we compared resting metabolic rate at thermoneutrality (RMRt), summit metabolic rate (M_{sum}) and heat loss (conductance) in adult and juvenile snow buntings on their summer and winter grounds. In summer, when buntings are in the Arctic, juveniles had a 12% higher RMRt, likely due to unfinished growth, and lost 14% more heat to the environment than adults. This pattern may result from juveniles fledging early to avoid predation at the cost of lower feather insulation. Surprisingly, an opposite pattern was observed at lower latitudes on their wintering grounds. Although they showed no difference in RMRt and M_{sum}, adults were losing 12% more heat than juveniles. We suggest that this difference is due to poorer insulative property of plumage in adults stemming from energetic and time constraints encountered during their post-breeding molt. High plumage insulation in first-winter juvenile buntings could be adaptive to reduce thermoregulatory demands and maximize survival in the first winter of life, while adults could use behavioral strategies to compensate for their greater rate of heat loss.

Keywords Arctic breeding · Wintering · Growth and development · Thermoregulation · Metabolic rate · Molt

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Introduction

For altricial bird species, rapid nestling growth limits vulnerability to nest predation (e.g. Cheng and Martin 2012; Martin 1995; Naef-Daenzer and Grüebler 2016; Remeš and Matysioková 2016). A direct consequence of this trade-off is that nestlings must invest large amounts of energy into body development to fledge at a younger relative age, often before they reach adult body mass (Cheng and Martin 2012; Naef-Daenzer and Grüebler 2016; Remeš and Matysioková 2016). Indeed, nestlings frequently leave the nest before completing growth and continue being fed by adults (Russell 2000). For example, Naef-Daenzer and Grüebler (2016) showed that among 65 ground and cavity-nesting passerine species, nestlings fledged at approximately 60% and 93% of adult body mass, respectively. Other studies reported nestlings leaving the nest with structural body growth 50–70% complete, although some traits such as tarsus length may be

comparable to that of adults (e.g. Cheng and Martin 2012; Portelli 2016; Stienen and Brenninkmeijer 2002). As growth is energetically demanding (Drent and Daan 1980; Vézina et al. 2009b; Ton and Martin 2016), recently fledged juveniles thus need to invest a certain proportion of their energy budget in the last stages of development.

Feather growth is typically incomplete immediately after fledging in birds. Cheng and Martin (2012) found wing length at fledging to be 60–90% of adult length in all 12 passerine species they studied. Contour feathers have also been reported to differ between juveniles and adults birds (Butler et al. 2008; Callan et al. 2019). For example, Rintamäki et al. (1983) reported higher thermal conductance (i.e., the rate at which heat is transferred from the body to the environment (McNab 1980)) in juvenile black grouse (*Lyrurus tetrix*) compared to adults in autumn, an indication of lower insulative property of contour plumage (Walsberg 1988; Wolf and Walsberg 2000). Higher thermal conductance was also reported during the first winter of life in blue tits (*Cyanistes caeruleus*) (Andreasson et al. 2020) and in Svalbard ptarmigan (*Lagopus muta hyperborean*) (Nord and Folkow 2018).

Lower insulation in juveniles likely adds to the energetic cost of post-fledging growth as increased heat loss creates additional energy demands for thermoregulation. This is important for species breeding at northern latitudes such as the Arctic, where relatively cold conditions or even snow storms can occur during the breeding season (Meltofte 1983; Hahn et al. 1995; Astheimer et al. 1995; Serreze and Barry 2014). Furthermore, some of these species, like snow buntings (*Plectrophenax nivalis*) and hoary redpolls (*Acanthis hornemanni*) winter in cold snowy environment (Brooks 1968; Montgomerie and Lyon 2020) and experience high thermoregulatory demands for most of the year. Comparing data for ten passerine species, Robinson et al. (2007) showed that adverse weather on temperate wintering grounds had a negative impact on survival, with greater effects on first-year individuals than adults. As juveniles may be less efficient at foraging (Weathers and Sullivan 1989; Wunderle 1991), their plumage insulation is therefore paramount as greater heat loss (Stettenheim 1972; Walsberg 1988; Wolf and Walsberg 2000) may also contribute to reduced survival during the first winter of life.

Arctic passerines are known to have remarkable adaptations for life in the cold (Meltofte 1983; Ryzhanovsky 2015). For example, Le Pogam et al. (2020) recently reported impressive cold endurance in wintering snow buntings with adult birds reaching their maximal shivering heat production at air temperatures estimated at −94 ℃. These birds also appear to maintain a cold-acclimated phenotype through migration and summer months as a potential adaptation to face unexpected cold spikes (Le Pogam et al. 2021a, b). With such adaptations for life in the cold, one would expect juveniles of Arctic species to be as well prepared as adults

for these conditions since leaving the nest early with suboptimal insulation and concomitantly having to invest energy in growth (Rintamäki et al. 1983; Callan et al. 2019) could be counter-adaptive. Juvenile snow buntings are known to fledge at 80–84% of adult body mass with primary and rectrix feathers shorter than that of adults (Maher 1964; Hussell 1972). They also have a rapid growth period with nestlings leaving the nest at 13 days on average (Maher 1964). It is unknown, however, whether juvenile buntings experience higher levels of heat loss than adults after fledging and whether this persists over the first winter of life.

Working with a snow bunting population at the northern boundary of their breeding range (Alert, NU, Canada 82°N), we examined morphological traits and metabolic variation in juvenile buntings in the weeks following fledging and compared it to that of adults. Given that buntings fledge before achieving adult size and mass, we expected higher maintenance energy consumption (basal metabolic rate (BMR), Swanson et al. 2017) in juveniles than in adults as young birds should still be investing energy in the last stages of growth (Rintamäki et al. 1983). We also expected one of two potential scenarios regarding juvenile plumage insulation. Snow buntings could show a pattern similar to that of other species (Rintamäki et al. 1983; Nord and Folkow 2018; Andreasson et al. 2020) with juveniles experiencing greater heat loss (i.e., higher thermal conductance) than adults, indicating elevated thermoregulation costs after fledging. Alternatively, given the species adaptations for life in the cold (e.g. Le Pogam et al. 2020, 2021a), snow buntings could fledge with insulation levels comparable to that of adults, which would suggest that this Arctic species is adapted for minimizing post-fledging energy demands for thermoregulation. High insulation would promote better energy efficiency for finalizing growth and for surviving their first winter. We also included a comparison of phenotypes between adults and first-winter juveniles captured on their wintering grounds in Québec, Canada, to investigate whether potential differences in traits remain over the first winter of life in snow buntings.

Material and methods

Comparing phenotypes on the breeding and wintering grounds

We captured forty-nine snow buntings (31 adults and 18 juveniles) at the Canadian Forces Station Alert, Nunavut (82°30′05″ N, 62°20′20″ W) in the Canadian High Arctic between May and August 2019 (Fig. 1). Adults were captured using either walk-in traps baited with mixed seeds before breeding, double potter traps with a live male decoy and territorial playback on their breeding territory or at
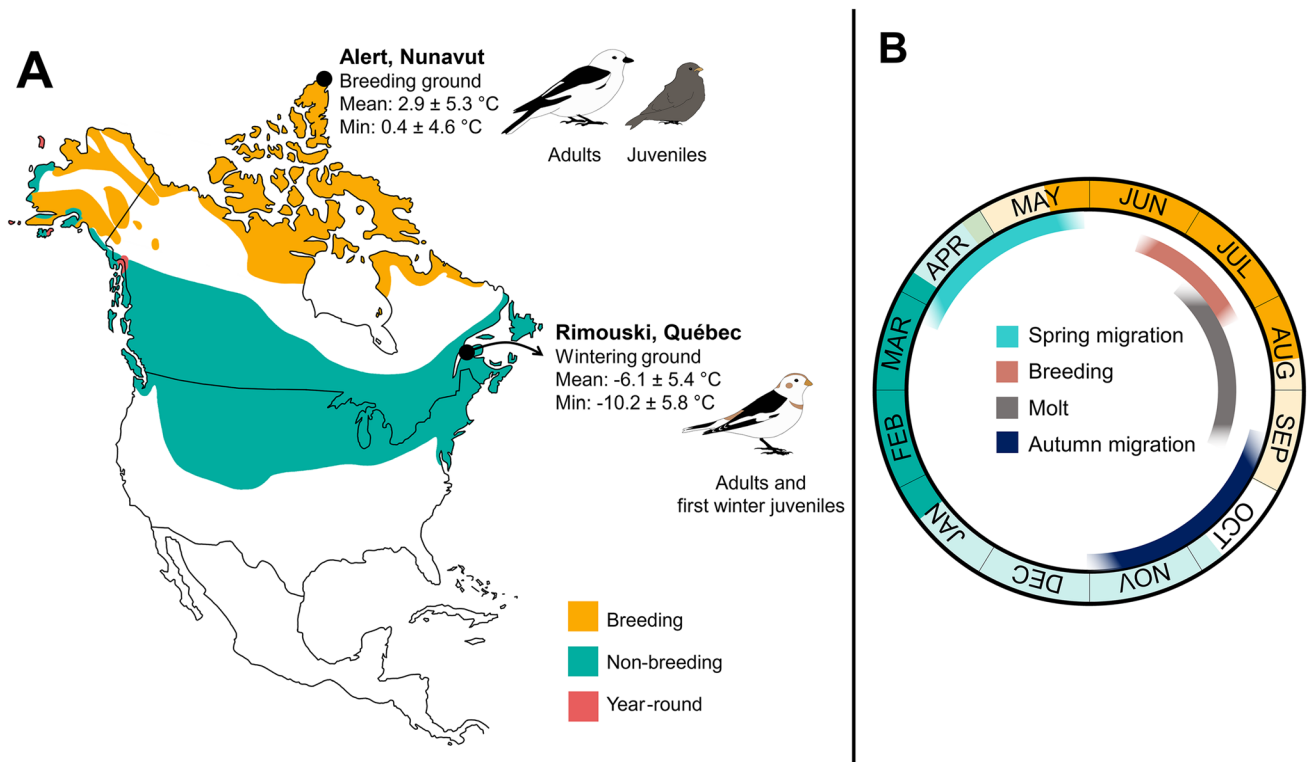
Fig. 1 Snow bunting distribution and location of summer and winter study sites (**A**). Note that snow buntings are associated with snow cover in winter and may not be observed in areas of their southern wintering range where snow is absent during warm winters. Temperatures presented are averages for the periods of captures. Snow bunting annual cycle (**B**). Colored months (darker) represent months where their nest while provisioning nestlings. Juvenile birds were captured using walk-in and potter traps baited with seeds between 19 July and 18 August. Although it was not possible to determine the time since fledging for juveniles, the last observed fledging event recorded in 2019 took place on July 24th. Recaptures of fledged juveniles in 2015, 2018 and 2019 also suggest that our captures and measurements were conducted during a period where structural growth was not completed as indicated by the length of the head plus beak (Fig. 2). All juveniles were in their first plumage and had not begun their postjuvenal molt (Pyle 1997; K. G. Young personal observation, 2020). Immediately after capture, we weighed birds (± 0.01 g) and took morphometric measurements on the head plus beak (± 0.01 mm), tarsus (± 0.01 mm), wing (± 0.1 cm) and tail (± 0.1 cm). We then brought the birds back to the field laboratory for respirometry trials (RMRt, see the metabolic performance below, $n=49$; conductance, $n=35$) and ultrasonography. Birds were kept in captivity for an average of 0.5 ± 0.5 days before RMRt and 1.9 ± 1.6 days before conductance trials before being released.

our data were collected on breeding and wintering sites, while lighter-colored months represent months where snow buntings are present at the site. Information presented is based on field observations, Macdonald et al. (2012), McKinnon et al. (2016), Montgomerie and Lyon (2020) and eBird (2023)

We also captured snow buntings (87 adults and 102 juveniles) during the winter months (January to April) from 2016 to 2018 in open fields near Rimouski, Canada (48°20′49″N, 68°43′32″W), using walk-in traps baited with cracked corn. Although they had completed their postjuvenal molt before their autumn migration, buntings in their first winter of life were categorized by plumage as wintering juveniles (Fig. 1). They were easily distinguished from adults using the coloration patterns of their flight feathers and wing covers (Pyle 1997; Love et al. 2012). We weighed and measured the birds as noted above and then transported them to the avian facilities of the Université du Québec à Rimouski for RMRt and conductance measurements (RMRt, $n=99$; conductance, $n=51$) and ultrasonography. Additionally, we measured the summit metabolic rate (M_{sum}), an indicator of shivering cold endurance (Swanson 2001; Swanson and Liknes 2006, see Le Pogam et al. 2020, 2021a) on 75 birds. The birds were kept in indoor cages (117 cm × 39 cm × 31 cm) for an average of 2.4 ± 1.7 days before both RMRt and M_{sum} and for 1.6 ± 0.9 days before conductance with ad libitum access to mixed seeds and water between metabolic trials and until being released.
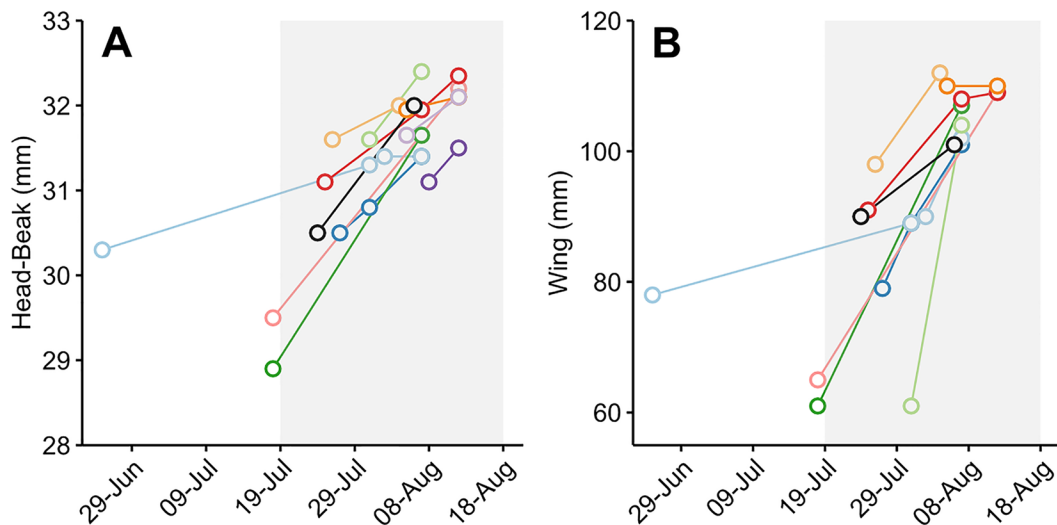
Fig. 2 Change in the length of (**A**) head plus beak and (**B**) wing over time in juvenile snow buntings (*Plectrophenax nivalis*) captured repeatedly in the Arctic. The gray area represents the period of the capture of juveniles in summer 2019

It should be noted that the wintering range of snow buntings breeding at Alert is unknown as no birds banded at Alert have been recovered in winter yet. However, while the population wintering in eastern Québec is known to breed in western Greenland (Macdonald et al. 2012), recent evidence based on the genetic signature of blood cells also suggests that birds from Alert are likely mixing with buntings breeding in the low Arctic (East-Bay, Southampton Island) and wintering in the Canadian prairies and, to a lesser degree, Ontario (Macdonald et al. 2012, 2016; Patel 2022). Wintering environmental conditions for these birds are comparable to that experienced by birds wintering in Eastern Québec.

Fat score and flight muscle size

We estimated fat reserves and flight muscle size in all buntings using visual scores. Fat score ranged from 0, (no visible fat), to 6, (tracheal pit is full and bulging with fat; Canadian Snow Bunting Network 2012; Gosler 1996). The scores for flight muscles were based on muscle shape and ranged from 0 (muscle depressed and the sternum is sharp) to 3 (muscles rounded above the sternum; Bairlein 1995; Busse 2000).

We also estimated the size of flight muscles non-invasively by measuring muscle thickness with ultrasonography (Royer-Boutin et al. 2015; Le Pogam et al. 2020, 2021a). Flight muscle thickness and keel height were measured on all adults and 12 juveniles in summer and on 37 adults and 48 juveniles in winter using a LOGIQe ultrasound scanner fitted with a linear probe (12 MHz, GE Healthcare,

Wauwatosa, WI, USA, see Le Pogam et al. 2020). Muscle thickness was obtained from a cross-sectional image by measuring, at 45° relative to the keel, the length between the muscle surface and the base of the bone. We included keel height as a covariate in statistical analyzes to control for variation in muscle thickness generated by the positioning of the probe (Le Pogam et al. 2020). Each measurement was repeated three to four times and average values were used in the analyses.

Metabolic performance

Physiological maintenance costs are measured as basal metabolic rate (BMR) in birds (Swanson et al. 2017). However, by definition BMR refers to animals not involved in generating new tissues (e.g. growth). Although our measurements respected the experimental standards for BMR (resting phase of the day, thermoneutrality, postabsorptive state), our juvenile birds were in the last stages of growth. We, therefore, use the term resting metabolic rate at thermoneutrality (RMRt) for both adults and juveniles in this study to avoid confusion. We performed summer measurements of RMRt and conductance at Alert using the instruments and setup described by Le Pogam et al. (2021b) and O'Connor et al. (2021). We used the instruments and setup described by Le Pogam et al. (2020, 2021a) for winter measurements of RMRt, conductance and M_{sum} at UQAR. As these methods have been described in detail previously, they are presented briefly below.

RMRt and conductance

At Alert, we placed buntings in 1.5L stainless steel metabolic chambers and pushed dry CO_2-free air (scrubbed with Silica gel, Soda lime and Drierite) at a constant rate of 650 ml·min^{-1}, controlled by mass flow controllers (Omega FMA5418A, previously calibrated with a Bubble-O-Meter), for both RMRt and conductance measurements. The excurrent chamber airstream was scrubbed of water vapor and CO_2 before entering one of the two FoxBox oxygen analyzers, each able to monitor two chambers in alternance using a MUX multiplexer (Sable Systems, Las Vegas, NV, USA). During RMRt trials, the airstreams sent to the analyzers alternated between a baseline channel (scrubbed ambient air) for 10 min and chamber channels. We measured up to 4 birds at a time (2 chambers per analyzer) for 40 min between baselines or for 60 min when analyzers were each monitoring a single chamber. We sampled the fractional oxygen concentration ($\dot{V}O_2$) in the excurrent airstreams every 20 s. On average, buntings were fasted for 4.76 ± 2.86 h prior to measurements. We measured RMRt overnight, lasting on average 9.4 ± 3.7 h. We measured conductance during the day (mean fasting time of 1.94 ± 0.58 h), on a maximum of 4 birds in parallel. On average, conductance measurements lasted 3.0 ± 0.05 h. We used the same protocol as for RMRt except that baseline air was measured for 10 min before and after chamber measurements, which lasted 160 min. During conductance measurements $\dot{V}O_2$ was sampled at a rate of 5 s. We measured chamber temperatures every 5 s with copper-constantan thermocouples (TC-2000 thermocouple reader, Sable Systems, Las Vegas, NV, USA). We maintained chamber temperature during RMRt trials at a thermoneutral temperature of 25 °C (Scholander et al. 1950). For conductance, adults were exposed to -20.6 ± 1.0 °C and juveniles were exposed to -8.4 ± 1.3 °C, both below the lower critical temperature of 10 °C for this species (Scholander et al. 1950).

At UQAR, we placed the birds in the same 1.5L metabolic chambers for measurements, which were also supplied with dry, CO_2-free air. Flow rates, controlled by mass flow controllers (Sierra Instruments, SideTrak®, Monterey, CA, USA), were 650 and 700 ml.min^{-1} for RMRt and conductance, respectively. This system can measure air coming from 4 chambers in parallel, using a 4 channel Servomex gas purity analyzer (model 4100, Boston, MA, USA). We, therefore, used an alternating sequence of 10 min baseline and 40 min chamber for RMRt (at 25 °C), which lasted 12.9 ± 2.3 h overnight (after 6.66 ± 2.54 h fasting). For conductance, chamber measurements lasted 100 min in total and baseline air was measured for 10 min three times during a sequence *i.e.*, the first 10 min, after 40 min of chamber measurement and after a further 60 min of chamber measurement. Birds were fasted for 1.75 ± 0.66 h before

conductance and metabolic chambers were maintained at -21.4 ± 6.8 °C during trials.

Summit metabolic rate

We used the same metabolic chambers for M_{sum}. During a trial, birds were first exposed to scrubbed air for 10 min at a flow rate of 1200 ml.min^{-1}, after which chamber inflow was replaced by a Helox gas mixture (21% oxygen, 79% helium) to increase heat loss (Rosenmann and Morrison 1974, mass flow controllers were calibrated for Helox using a Bubble-O-Meter). After 5 min at -18 °C, birds O$_2$ consumption was measured and we subsequently dropped chamber temperature by 3 °C every 20 min (Swanson et al. 1996) until the birds showed signs of hypothermia (indicated by a decline in O$_2$ consumption for several minutes) or reached the end of a 185 min automated program (see Le Pogam et al. 2020). Summit metabolic rate measurements lasted for 1.92 ± 0.67 h and birds were not fasted prior to measurements.

We weighed snow buntings before and after all metabolic measurements and average body mass was used in analyses. We also measured body temperature (T_b) for conductance and M_{sum}, just before entering and immediately after exiting metabolic chambers, by inserting a type-T thermocouple approximately 10 mm into the cloaca (Omega model HH-25KC, NIST-traceable, Omega, Montréal, QC, Canada). We conducted respirometry calculations, for both summer and winter, with ExpeData V.1.8.4 (Sable Systems, Las Vegas, NV, USA), using the lowest averaged 10 min of $\dot{V}O_2$ for conductance and RMRt and the highest averaged 10 min of $\dot{V}O_2$ for Msum. Oxygen consumption was calculated using Eq. 10.1 from (Lighton 2019) and then converted to watts using a thermal equivalent of 19.8 kJ·L^{-1}O$_2$ (representing an assumed respiratory quotient of 0.71) (Gessaman and Nagy 1988). Conductance was calculated as

$$C = \mathrm{MR}/(T_b - T_a),$$

where MR = metabolic rate, T_b = average body temperature and T_a = average ambient temperature in the chamber during the lowest 10 min $\dot{V}O_2$.

Statistical analysis

We used permutation tests for linear models (LMP) using the lmPerm package (Wheeler and Torchiano 2016) to assess morphological differences between adults and juveniles at Alert and between adults and first winter birds captured on their wintering grounds in Rimouski. Permutation tests were used because the distribution of residuals for some morphometric variables deviated from normality. Permutation tests for

linear models compared traits (body mass, length of the head plus beak, tarsus, wing, tail as well as fat and muscle scores) between age classes (adults and juveniles). For structural size variables, models also included the fixed factor "observer" to control for potential measuring bias among observers. As winter data were collected over three winters, we also added "year" as a fixed factor in models comparing wintering birds. We then performed post-hoc pairwise comparisons between years using permutation *t*-tests when the year effect was significant. For variables with a normal distribution of residuals, the results obtained from the LMP were very similar to those

obtained with linear models and led to the same conclusions. We, therefore, used LMP throughout for consistency. We used ANCOVA models, with body mass as a covariate, to assess whether RMRt, conductance and M_{sum} differed between age classes within seasons.

All analyses were conducted in the R 4.1.1 (R Core Team 2021) environment, and we confirmed the normality of residuals visually for analyses on metabolic traits. For permutation tests, the exchangeability postulate was met as our morphometric measurements could belong to any age class under the null hypothesis (*i.e.*, no difference between
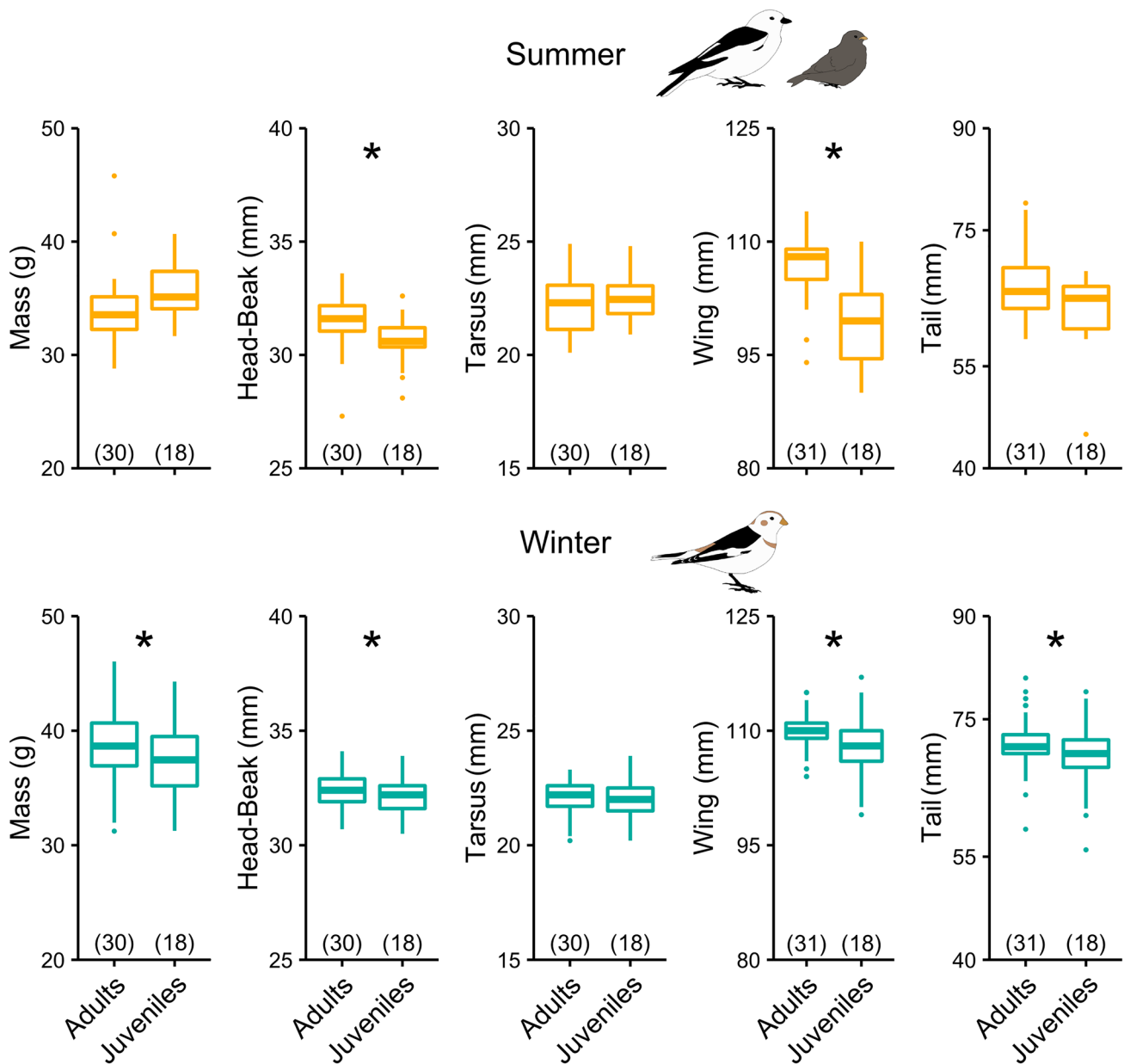

Fig. 3 Age differences in morphometric measurements in summer 2019 (Arctic) and winter 2016–2018 (Québec). Numbers in parentheses are sample sizes

adult and juvenile traits). This assumption can be made with observational data such as ours (Anderson 2001). Data are presented as mean ± s.e.m.

Results

Comparing juveniles and adults in summer—Arctic

Our data revealed that, at the time of capture, juveniles had a body mass similar to adults but had yet to complete feather growth and the development of some structural traits (Fig. 3). Specifically, the length of the head plus beak in juveniles was $97.5 \pm 0.8\%$ of that measured in adults ($N_{perm} = 5000$, $P = 0.02$), and the same pattern was apparent for wing length ($93.0 \pm 1.3\%$, $N_{perm} = 5000$; $P < 0.0001$) and tail length ($95.6 \pm 2.0\%$, $N_{perm} = 1500$; $P = 0.06$). We found no evidence that body mass and tarsus length differed among age class ($N_{perm} = 681$; $P = 0.1$ and $N_{perm} = 247$; $P = 0.3$ respectively).

We observed no significant difference in fat score between juveniles and adults ($N_{perm} = 51$; $P = 0.8$), although muscle scores were higher, on average, in juvenile birds (adults $= 1.6 \pm 0.5$; juveniles $= 1.9 \pm 0.3$; $N_{perm} = 2875$; $P = 0.03$). However, this difference did not transpose into muscle thickness as measured by ultrasonography ($N_{perm} = 154$; $P = 0.4$).

Resting metabolic rate at thermoneutrality and conductance increased with body mass in both juvenile and adult snow buntings (mass effect: RMRt: $P < 0.0001$, conductance: $P = 0.01$) (Fig. 4). For a given body mass, RMRt was $11.7 \pm 2.3\%$ higher in juvenile birds compared to adults ($F_{1,46} = 11.59$; $P = 0.001$) (Fig. 4a). Young buntings also lost more heat to the environment for their mass than adults, with conductance being $11.3 \pm 3.5\%$ higher in juveniles than in adults ($F_{1,32} = 4.60$; $P = 0.04$) (Fig. 4b).

Comparing first winter birds and adult buntings in winter—Québec

We found a significant difference in body mass between age classes in winter. First winter buntings were, on average, $2.8 \pm 0.8\%$ lighter than adults ($N_{perm} = 5000$; $P = 0.001$) (Fig. 3). We also observed a significant year effect on body mass ($N_{perm} = 5000$; $P = 0.01$) with birds being heavier in 2018 ($N_{perm} = 999$; $P = 0.024$ for comparisons with both 2016 and 2017). There were slight differences in structural size between age classes. Indeed, the length of the head plus beak in first winter birds was $99.1 \pm 0.2\%$ of that measured in adults ($N_{perm} = 4160$; $P = 0.02$) (Fig. 3). Our results further showed that wings and tail feathers were significantly shorter during the first winter of life compared to adults (no difference in tarsus length $P = 0.24$, $N_{perm} = 325$). Wing and tail lengths were respectively $98.2 \pm 0.3\%$ ($N_{perm} = 5000$; $P < 0.0001$) and $98.1 \pm 0.6\%$ ($N_{perm} = 5000$; $P = 0.007$) of adult size (Fig. 3).

There was no significant difference in fat reserves carried by adults and wintering juveniles ($N_{perm} = 306$; $P = 0.25$) and both had similar flight muscles sizes (Score: $N_{perm} = 87$, $P = 0.54$, thickness: $N_{perm} = 99$, $P = 0.50$). However, muscle scores did differ among years ($N_{perm} = 5000$; $P < 0.0001$, pectoral thickness $P = NS$) with higher muscle scores observed in 2018 relative to the two previous years ($N_{perm} = 999$; $P = 0.003$ for comparison with both 2016 and 2017).

Considering the significant influence of body mass on RMRt ($F_{1,96} = 33.19$; $P < 0.0001$) and M_{sum} ($F_{1,72} = 18.22$; $P < 0.0001$), winter metabolic performance did not differ between first winter snow buntings and adults (age effect $P > 0.10$ in both RMRt and M_{sum}). In contrast, winter conductance varied independently from body mass (mass effect $P = 0.3$) with adults losing $12.3 \pm 3.4\%$ more heat on average than juveniles ($F_{1,48} = 7.61$; $P = 0.008$) (Fig. 5).

Fig. 4 Resting metabolic rate at thermoneutrality (RMRt) (**A**) and conductance (**B**) as a function of body mass in snow buntings during summer (Arctic). Linear regression in adults ($n = 31$; 22) is represented by the solid line and the dashed line represents linear regression for juveniles ($n = 18$; 13)
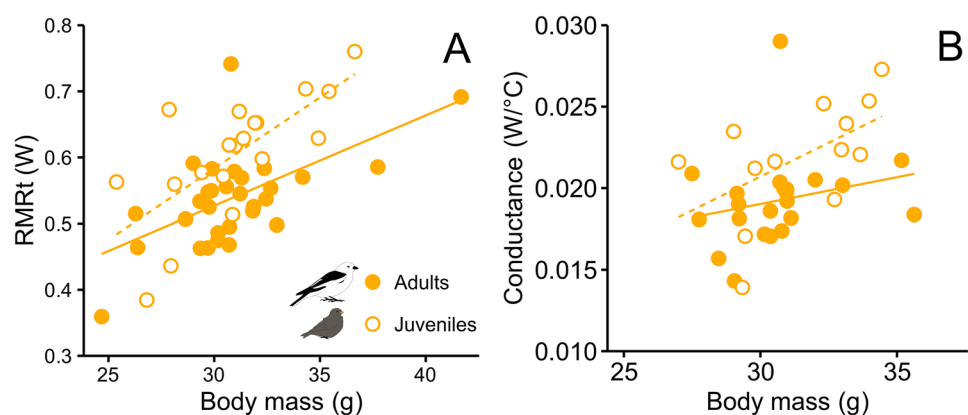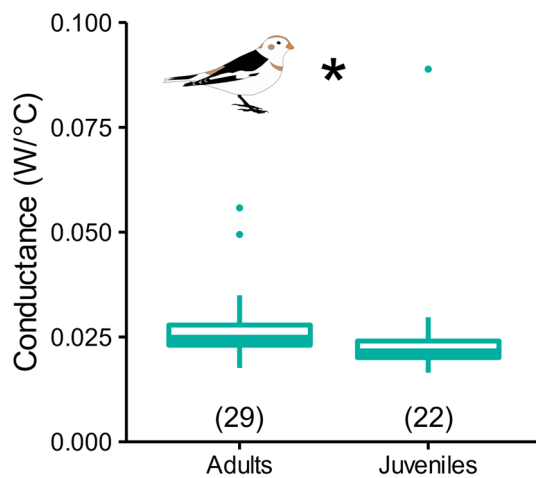
Fig. 5 Age difference in mean conductance during winters 2016 to 2018 (Québec). Numbers in parentheses are sample size

Discussion

In this study, we examined whether juvenile snow buntings in their last stages of growth experience elevated maintenance costs relative to adults and compared body heat loss between juveniles and adults. Our data from the Arctic show that recently fledged juveniles had not completed structural growth at the time of capture based on differences in wing and head plus beak length. Juveniles also experienced a 12% higher resting metabolic rate relative to adults, which is consistent with juveniles investing more energy in growth following fledging (Rintamäki et al. 1983). We further observed that recently fledged juvenile buntings in the Arctic had a rate of heat loss of 14% higher than that of adults, which suggests that, despite being a cold specialized species, buntings display similar trends to passerines breeding at lower latitudes regarding plumage insulation (e.g. Andreasson et al. 2020). Comparing snow bunting age classes in winter revealed similar metabolic performance in adults and first-winter birds. However, heat loss was 12% higher in adults, a pattern opposite to that observed on the breeding ground.

Juveniles and adults in summer—Arctic

While juvenile snow buntings had body mass and fat stores comparable to adults, they fledged before fully completing their feather and structural body growth. Snow buntings are known to fledge before reaching adult size (see Fig. 2) and continue to grow their remiges and rectrices even after starting their postjuvenal body molt (Maher 1964; Hussell 1972). This pattern is consistent with other passerines where nestlings typically leave the nest before finalizing growth (Cheng and Martin 2012; Portelli 2016; Remeš et al. 2020),

likely to reduce nest predation risk (Naef-Daenzer and Grüebler 2016; Remeš and Matysioková 2016). In fact, despite snow buntings nesting inside enclosed structures, such as rock cavities (Montgomerie and Lyon 2020), Hussell (1972) reported heavy nest predation by arctic foxes (*Alopex lagopus*) and weasels (*Mustela erminea*) on Devon Island. These two predators are also present in Alert.

We found that juvenile snow buntings had larger flight muscles than adults based on visual scores, although this did not translate into differences in muscle thickness. This is likely due to scores evaluating the 3-dimensional shape of muscles, whereas ultrasonography measures muscle thickness cross-sectionally, which may underestimate muscle volume differences (Swanson and Merkord 2013; Vézina et al. 2021; see also Royer-Boutin et al. 2015). Larger flight muscles in juvenile buntings could be a response to higher wing loading as they must fly with similar mass but with shorter wings than adults. Lind and Jakobsson (2001) also showed that molting tree sparrows (*Passer montanus*) increased their pectoral muscle size to body mass ratio with an increase in wing loading.

We found 11% higher conductance in juveniles compared to adult buntings at Alert, a finding compatible with observations by Andreasson et al. (2020) in blue tits and by Rintamäki et al. (1983) in black grouse. Higher conductance in juveniles likely reflects feather structural differences and lower feather mass relative to adults, as reported by Butler et al. (2008) for 10 species of warblers. Additionally, Butler et al. (2008) found a positive correlation between feather quality (based on barb count and feather mass) and duration of the nestling period among these species, suggesting that some may trade off feather insulation for early fledging. Callan et al. (2019) observed similar cost–benefit trade-offs between feather quality (based on barb density) and nestling duration among 123 temperate and tropical species. With juvenile snow buntings fledging at 13 days on average (Maher 1964), the benefit of fledging early (e.g., predator avoidance) may outweigh the cost of lower insulation and the accompanying thermoregulatory disadvantages during unpredictable cold days. Furthermore, the insulative property of feathers grown in the nest also depends on the timing of their renewal (i.e., feather lifespan) (Kiat and Sapir 2018). As juvenile buntings go through a complete molt of body feathers before their fall migration (Hussell 1972), low insulation would thus only be an ephemeral constraint as they could improve insulation before departure. Thus, the fitness costs of producing ephemeral body feathers with poor insulative properties is likely outweighed by the fitness benefits of a shorter development time (Callan et al. 2019), which is crucial in Arctic species experiencing short favorable conditions for breeding. Furthermore, juvenile buntings do fledge with a

dark grey plumage which may partly compensate for heat loss by maximising heat gain from solar radiation, often 24 h per day in the high Arctic. Additionally, juvenile buntings could compensate for higher heat loss in summer by increasing shivering heat production capacity (Swanson 2010; Mckechnie and Swanson 2010; Le Pogam et al. 2020, 2021a), and this could be associated with larger flight muscles as observed here (O'Connor 1995; Dubois et al. 2016; Le Pogam et al. 2020).

Resting metabolic rate was 12% higher in juvenile buntings than in adults of comparable mass. This is likely not a thermal acclimation response (cf. Vézina et al. 2009b) as we found no correlation between conductance and RMRt in birds measured at Alert (data not shown). Given that juveniles still had to complete feather development and part of structural growth at the time of capture (Fig. 2), and that growth rate is known to correlate with BMR in other passerines (Ton and Martin 2016; see also Vézina et al. 2009a), the higher RMRt in juvenile buntings could reflect energy invested in the last stages of growth after fledging, including internal organ development and tissue maturation. For example, post-fledging development of organs has been reported in altricial domestic pigeons (*Columba livia*) (Liang et al. 2018) as well as in precocial greater snow geese (*Chen caerulescens atlantica*) (Lesage and Gauthier 1997). Vézina et al. (2009a) further showed that some organs, such as the heart, kidney, pancreas, pectoral muscles and intestines, are still developing a few days before fledging in European starlings (*Sturnus vulgaris*). Higher metabolic rates have also been reported in nestlings house martin (*Delichon urbicum*) compared to adults (Prinzinger and Siedle 1988) and in fledged black grouse (Rintamäki et al. 1983).

Juveniles and adults in winter—Québec

Comparing adult and juveniles on the wintering grounds, we found differences in morphometric measurements. Juveniles had shorter head plus beak, wing and tails than adults. This corroborates findings by Meltofte (1983) and Smith (1994) who also reported shorter wings in juvenile snow buntings during the first winter of life compared to adults in Greenland and Scotland respectively (but see Banks et al. 1989; Rae and Marquiss 1989). In their first winter, juveniles were also on average 3% lighter than adults. As juveniles snow buntings are dominant over adults on the wintering ground, they have priority access to food and may store less fat reserves (Smith and Metcalfe 1994, 1997; Laplante 2018). This difference was not reflected in our fat score results however, which may be due to the relatively small difference between age classes. We further observed significantly heavier birds and higher muscles scores in 2018 compared to 2016 and 2017. Interestingly, 2018 was the year with the coldest winter, (lowest mean temperature = −10.8 ± 5.7 ℃) compared to −8.6 ± 5.3 ℃ in 2016 and −8.3 ± 6.1 ℃ in 2017. Laplante et al. (2019) showed that snow buntings increase their body mass and fat reserves in colder and snowier conditions. Thus, the year effect on body mass and muscle size observed here might result from colder temperatures requiring improved thermogenic capacity and larger fat reserves (Swanson and Olmstead 1999).

Surprisingly, juvenile buntings on their winter grounds lost 12% less body heat than adults. This suggests that first-winter juveniles become better insulated than adults following their postjuvenal molt on their breeding grounds. This differs from observations in blue tits where first-winter birds typically suffer greater heat loss than adults during the cold season (Andreasson et al. 2020). However, blue tits typically experience milder temperatures in winter than buntings. The reason for the switch in conductance patterns between juvenile and adults during breeding and wintering is not immediately obvious and could potentially be linked to population differences. However, it may also result from the timing of breeding and molt on the Arctic breeding ground. Indeed, adult snow buntings are known to begin molting while still provisioning nestlings (Hussell 1972; Green and Summers 1975; Montgomerie and Lyon 2020). In fact, post-breeding molt is very rapid (28 to 35 days Green and Summers 1975; Hussell 1972) and involves the loss of several flight feathers at once, which can lead to flightlessness (Parmelee 1968; Green and Summers 1975; Ryzhanovsky 2015; Montgomerie and Lyon 2020). As nestling provisioning and molt can be energetically demanding (Hussell 1972; Drent and Daan 1980; Walsberg 1983; Murphy and King 1992; Lindström et al. 1993), it is likely that adult snow buntings face energy and time constraints restricting the production of high-quality feathers. Furthermore, while both juveniles and adults molt into their winter plumage before departing the breeding grounds, adults have to carry out a complete post-breeding molt while post-juvenal molt is only partial, with body feathers and some secondary coverts being replaced (Hussell 1972; Pyle 1997; Ryzhanovsky 2015; Montgomerie and Lyon 2020). Time and energy constraints on molt have been observed before and can lead to the production of feathers with poorer insulative properties (Dawson et al. 2000; Hall and Fransson 2000; Koskenpato et al. 2016). For example, Nilsson and Svensson (1996) reported a trade-off between reproduction and molt in late-breeding blue tits that were found to spend more energy in thermoregulation the following winter. The negative effect of increased feather growth rate on feather structure was also observed in both juveniles (Butler et al. 2008) and adult passerines (Dawson et al. 2000; De La Hera et al. 2009). Therefore, no matter the location of their breeding ground, juvenile snow buntings appear less restricted than adults in producing their first

winter plumage and this could explain the better insulation observed in first year wintering individuals compared to adults. Nevertheless, the greater heat loss in adults does not appear to be offset by a higher thermogenic capacity (M_{sum}) or basal heat production (RMRt). This suggests that experienced wintering adults could rely on other means, such as behavioural thermoregulation, to reduce the impact of heat loss on their daily energy budget.

Author contributions RD and FV conceived the ideas and designed the study. ALP, KY and FV collected the data. RD analyzed the data. RD, AL, FV, RO, led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

Data availability Data are not available for this article.

Declarations

Conflict of interest The author(s) declare that they have no conflict of interest.

Ethical approval All bird handling at Rimouski and at Alert was approved by the Animal Care Committee of the Université du Québec à Rimouski (Rimouski: CPA-54-13-130 and CPA-71- 17-195 and Alert: CPA-61-15-163 and CPA-68-17-186) and was conducted under banding (10889) and scientific (SC-48, NUN- SCI-15-05) permits from Environment and Climate Change Canada, and under scientific permits from the Department of Environment of Nunavut (WL 2015-055, 2018- 010, 2019-002).

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