Ornithology

Wintering closer to breeding grounds comes at a cost in an Arctic-specialized songbird, *Plectrophenax nivalis* (Snow Bunting)

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ABSTRACT

Wintering at high latitudes may offer Arctic-breeding migratory birds advantages such as shorter migration distances and earlier arrival at breeding sites, potentially improving reproductive success. However, wintering at northern sites may also come at a cost as birds can experience colder and harsher conditions than individuals wintering farther south, consequently requiring physiological adjustments for life in the cold. We compared the physiological costs of wintering at different latitudes in *Plectrophenax nivalis* (Snow Bunting) from an Eastern Canadian population during the peak of winter. We hypothesized that individuals wintering at higher (i.e., colder) latitudes would be structurally larger, have better thermal insulation, maintain thicker pectoralis muscles and more lean tissues, carry larger lipid reserves, and experience greater physiological maintenance costs compared to individuals wintering at lower (i.e., warmer) latitudes. Contrary to our expectation, structural size did not differ between wintering sites. However, northern birds were 8% heavier and carried 32% more lipid reserves, suggesting increased energy storage for cold endurance. These birds also had 4% more lean mass and maintained slightly thicker pectoralis muscles, consistent with greater shivering thermogenesis capacity. Notably, basal metabolic rate (BMR), corrected for lean mass, was 6% higher in northern birds, indicating elevated physiological maintenance costs in colder environments. These findings therefore show that *P. nivalis* must pay a significant and measurable cost when wintering in colder environments to benefit from the potential fitness advantage of a shorter migration distance to their Arctic breeding grounds. Our study illustrates the physiological trade-off migratory birds face when selecting wintering locations and underscores the importance of considering both ecological benefits and metabolic costs when studying avian life-history strategies under variable climatic conditions.

Keywords: Arctic passerines, body composition, cold wintering site, differential migration, latitude, physiological costs

LAY SUMMARY

- *Plectrophenax nivalis* (Snow Bunting) wintering in Eastern Canada are distributed along a southwest-to-northeast axis, with individuals occupying northeastern sites experiencing colder environments than those wintering in milder southwestern sites.
- Investigating physiological costs associated with winter distribution can help understand wintering site selection and its impact on other life-history stages such as breeding.
- We caught *P. nivalis* during winter at different latitudes (northern and southern sites) and compared physiological traits such as body mass, body composition, flight muscles size, and metabolic rates.
- Birds wintering at higher latitudes were heavier, carried more lipids and lean tissues, had larger flight muscles and higher physiological maintenance costs measured as metabolic rates.
- Results suggest that, while northern wintering *P. nivalis* might benefit from shorter migration distance to their breeding grounds in the spring, they nevertheless pay a measurable physiological cost to live in a harsher environment during the cold season.

"Passer l'hiver plus près des sites de reproduction a un coût chez un passereau spécialisé de l'Arctique, Plectrophenax nivalis (Plectrophane des neiges)."

RÉSUMÉ

Hiverner à des latitudes élevées peut offrir aux oiseaux migrateurs arctiques certains avantages, comme une distance de migration plus courte et une arrivée plus précoce sur les sites de reproduction, ce qui pourrait améliorer leur succès reproducteur. Toutefois, hiverner plus au nord expose également ces oiseaux à des conditions climatiques plus froides et rigoureuses, nécessitant des ajustements physiologiques. Nous avons comparé les coûts physiologiques de l'hivernage à différentes latitudes chez **Plectrophenax nivalis** (Plectrophane des neiges), issu d'une population de l'est du Canada, durant le cœur de l'hiver. Nous avons émis l'hypothèse que les individus hivernant à des latitudes élevées (et donc plus froides) seraient de plus grande taille, mieux isolés thermiquement, avec des muscles pectoraux plus développés, davantage de tissus maigres, des réserves lipidiques plus importantes et des coûts physiologiques de maintenance plus élevés que ceux hivernant plus au sud. Contrairement à nos attentes, la taille corporelle ne variait pas selon le site d'hivernage. Cependant, les oiseaux hivernant plus au nord étaient 8% plus lourds et possédaient 32% de réserves lipidiques en plus, suggérant une stratégie de stockage énergétique accrue pour résister au froid. Ils avaient également 4% de masse maigre supplémentaire et des muscles pectoraux légèrement plus épais, indiquant une meilleure capacité de thermogenèse par frissonnement. Le taux métabolique basal, corrigé pour la masse maigre, était 6% plus élevé chez les individus hivernant davantage au nord, traduisant un coût physiologique de maintenance accru en milieu froid. Ces résultats montrent que *P. nivalis* supporte un coût physiologique mesurable lorsqu'il hiverne dans des environnements plus froids, en échange du potentiel avantage d'une migration plus courte vers les sites de reproduction arctiques. Notre étude met en évidence le compromis physiologique auquel font face les oiseaux migrateurs dans la sélection de leurs sites d'hivernage et souligne l'importance de considérer à la fois les bénéfices écologiques et les coûts métaboliques dans l'étude des stratégies d'histoire de vie aviaire en contexte climatique variable.

Mots-clés: Composition corporelle, coûts physiologiques, latitude, migration différentielle, passereaux arctiques, site d'hivernage froid

INTRODUCTION

Migration is described as a seasonal movement of populations between regions where conditions alternate between favorable and unfavorable (Dingle and Drake 2007). Within these movements, differential migration refers to situations where distinct classes of individuals (age, sex, or subspecies) differ in one or more aspects of their migration, either distance, timing or both (Terrill and Able 1988, Cristol et al. 1999). Many hypotheses are still considered to explain differential migration (Paprocki and Conway 2024). In northern passerines, the typical pattern is heavier individuals (often males) wintering further north than lighter individuals (often females; *Junco hyemalis* [Dark-eyed Junco], Ketterson and Nolan 1976; *Zonotrichia leucophrys* [White-crowned Sparrow], Morton 1984; *Plectrophenax nivalis* [Snow Bunting], Macdonald et al. 2016). This geographical segregation thus results in different spring migration distances, with birds wintering at lower latitudes having longer distances to travel to reach their breeding grounds. Although wintering at northern sites is often associated with advantages such as early arrival on the breeding grounds (e.g., Rotics et al. 2018) that may help secure the best territories and lead to higher reproductive success (Møller 1994), this strategy may come with significant wintering costs.

In north temperate areas, wintering at high latitudes involves constraints associated with cold temperatures (Scholander et al. 1950, Cooper and Swanson 1994, Liknes and Swanson 1996), low food abundance (King 1972, McNamara et al. 1990, Swanson 2010, Carey 2012) and shorter days for diurnal species, which reduces feeding duration and increases fasting times. Life in the cold also typically translates into high feeding rates when food is available, to keep up with energetic demands (McWilliams et al. 1999, Williams and Tieleman 2000, Vézina et al. 2006a), as well as high rates of lipid accumulation to compensate for unpredictable access to food (Blem 1973, Gosler 2002, Laplante et al. 2019). As a result, individuals facing cold wintering conditions often have large energy-processing organs (Williams and Tieleman 2000, Petit et al. 2014, Wu et al. 2014) and pectoralis muscles, which are used in shivering thermogenesis (Cooper 2002, Liknes and Swanson 2011, Swanson and Merkord 2013). However, these changes often lead to elevated physiological maintenance costs (Wiersma and Piersma 1994, Piersma et al. 1996, Williams and Tieleman 2000, Cooper 2002), measured as basal metabolic rate (BMR, Swanson 2010). Thermal constraints and the resulting physiological responses can also vary among individuals differing in body size (Dawson et al. 1983, Marsh and Dawson 1989). In other words, the constraints and responses might be tempered to a certain degree in larger individuals, whose lower surface area to volume ratio may offer the benefit of lower relative heat loss compared to birds of smaller body size (Baldwin et al. 2023). Cold conditions can also translate into increased insulative properties of plumage (Saarela et al. 1989, Swanson 1991, Cooper 2002), potentially allowing best-insulated individuals to winter higher north in colder environments (Blem 1981; but see Stager et al. 2020). Plumage insulation is routinely measured as thermal conductance, which is the body heat transferred from an animal to its environment (McNab 1980, Hill et al. 2016).

As far as we know, the physiological consequences of differential migration have received little empirical attention in northern wintering passerines, especially over an array of physiological parameters (but see Nolan and Ketterson 1983). A good model species to study the relative physiological costs of differential migration at northern latitudes is *P. nivalis*. In North America, this Arctic-breeding passerine winters in cold, snowy, temperate regions (Rae and Marquiss 1989, Banks et al. 1991). This requires physiological adjustments for thermoregulation (Le Pogam et al. 2020) as well as lipid storage to support local variation in energy demands (Laplante et al. 2019). The Eastern North American population shows a southwest to northeast winter distribution (see Figure 1 in Macdonald et al. 2012). Along this axis, we observe a typical differential migration where most smaller females, and some small males, are found in the southwestern portion of the species' wintering range, whereas most larger males, and some large females, are found at higher eastern latitudes (Macdonald et al. 2016). Using banding recovery data, Macdonald et al. (2012) studied migratory connectivity of *P. nivalis* from Eastern Canada and showed that those birds breed in Greenland. Individuals wintering at northeastern sites are thus closer to their breeding
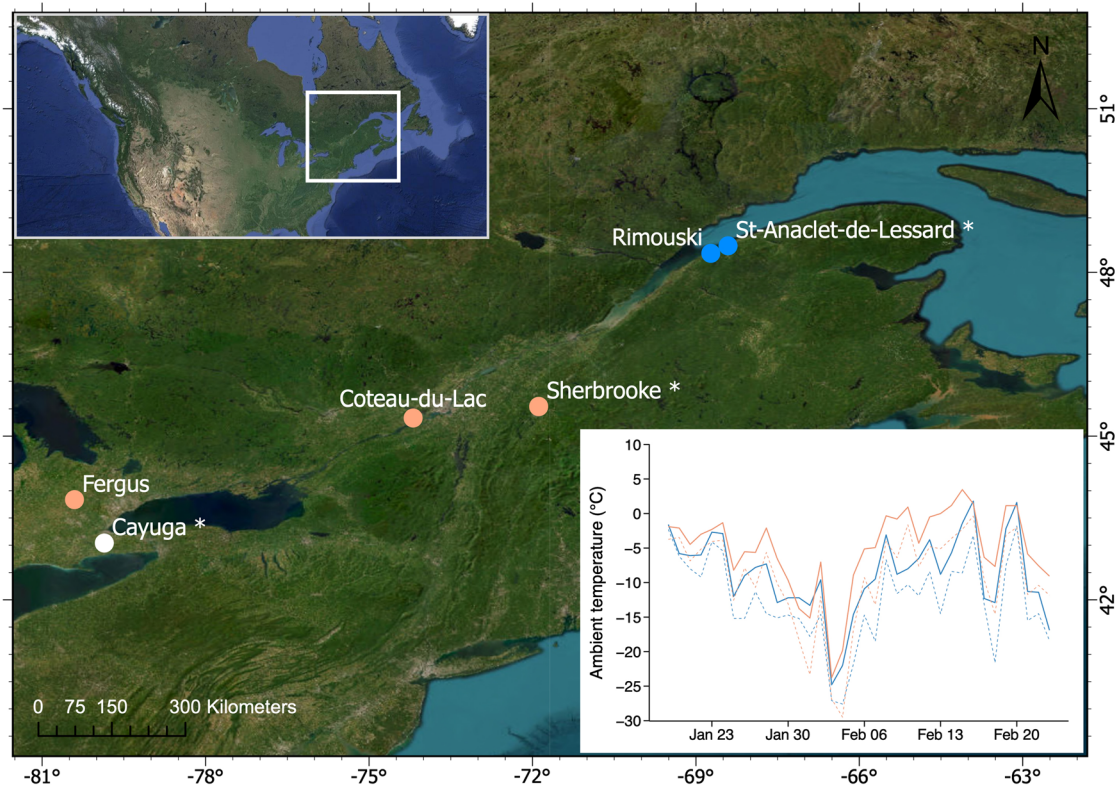
FIGURE 1. Geospatial extent of study area with capture locations of wintering *Plectrophenax nivalis* (Snow Bunting). Locations where a temporary laboratory was set up are designated with an asterisk (*). Capture locations are represented with colored circles (white = not used in statistical analyses, orange = southern sites, blue = northern sites). Mean daily (solid line) and mean minimum (dashed line) ambient temperatures during the sampling period (January 19 to February 23, 2023) for combined southern sites (Fergus, Coteau-du-Lac, and Sherbrooke; orange line) and Rimouski (blue line) are shown to highlight the temperature differences across the study area. No snow cover data was available for this study.

grounds and are thought to have shorter migration distances to travel in the spring (Macdonald et al. 2012). Males also arrive earlier than females on their breeding grounds (Guindre-Parker et al. 2013, Mckinnon et al. 2016), allowing them to quickly secure high-quality breeding territories (Guindre-Parker et al. 2013, Macdonald et al. 2016), which likely increases their reproductive success (Meltofte 1983, Guindre-Parker et al. 2013).

In this study, we examined the potential physiological costs of *P. nivalis* wintering in colder and harsher northern environments relative to presumably less physiologically costly southern areas. In addition to structural size and body mass, we documented the lean and lipid components of body mass, pectoralis muscle thickness and body insulation in addition to quantifying physiological maintenance costs (i.e., basal metabolic rate). We expected birds wintering at higher latitudes to be structurally larger (Ashton 2002, Olson et al. 2009, Macdonald et al. 2016) and heavier (Nolan and Ketterson 1983, Olson et al. 2009), to have larger pectoralis muscles (Cooper 2002, Liknes and Swanson 2011) and more lean tissues on average (Zheng et al. 2008, Petit et al. 2014), which should be associated with higher maintenance costs (Kendeigh and Blem 1974, Swanson 1990, Petit et al. 2014, Broggi et al. 2019) than individuals spending the winter at sites farther south. We also expected these birds to carry larger lipid stores (Blem 1976, Cooper 2007, Le Pogam et al. 2020). Finally, we predicted that individuals wintering at northern sites would also be those benefiting from greater plumage insulation relative to individuals experiencing milder southern conditions (Saarela et al. 1989, Swanson 1991, Cooper 2002).

METHODS

Study Sites

Plectrophenax nivalis in Quebec (QC) and Ontario (ON) are distributed along a southwest-to-northeast axis from the Great Lakes to the Gulf of St Lawrence (Macdonald et al. 2012, Montgomerie and Lyon 2020). Therefore, birds farthest to the northeast experience the most challenging wintering conditions, while those to the southwest are exposed to milder conditions (Figure 1; Laplante et al. 2019). We captured and measured birds at 6 different locations in Eastern Canada from January 19, 2023, to February 23, 2023: St-Anaclet-de-Lessard (QC), Rimouski (QC), Sherbrooke (QC), Coteau-du-Lac (QC), Cayuga (ON) and Fergus (ON) (Figure 1). We selected these locations to represent the thermal conditions in the wintering range of the Eastern Canadian *P. nivalis* population. We set up field laboratories at the extremes and mid-range locations across the wintering range (see Figure 1). For statistical reasons the northernmost locations (Rimouski and St-Anaclet-de-Lessard) were grouped as the "northern" sites and the remaining sites (Fergus, Coteau-du-Lac and Sherbrooke) as the "southern" sites (see the statistical analysis section).

Capture and Measurements Protocols

We captured birds at each site (Cayuga, *n* = 8; Fergus, *n* = 12; Coteau-du-Lac, *n* = 6; Sherbrooke, *n* = 7; Rimouski, *n* = 17; St-Anaclet-de-Lessard, *n* = 73) with walk-in or whoosh-net traps baited with commercially available crushed corn. Immediately after capture, we weighed (±0.01 g; i.e., body mass at

capture) the birds and aged and sexed them according to Pyle (1997). We then banded individuals with a USGS-numbered metal band and took morphometric measurements (lengths of wing, tail, tarsus and head + beak). We then transported the birds in individual fabric bags to an indoor temporary laboratory where they could undergo further measurement and be kept in cages (117 cm wide × 31 cm deep × 39 cm high) with access to food (crushed corn, wheat, sorghum, white and red millet, black oil sunflower; Armstrong, Hagersville, ON) and water ad libitum until further measurements.

Body Composition

Once in the laboratory, we re-weighed (±0.01 g) the birds before measurements and estimated the lipid and lean components of their body mass (southern sites, $n = 24$; northern sites, $n = 90$) to the nearest ±0.01 g using non-invasive quantitative magnetic resonance (QMR; EchoMRI, Houston, TX; Guglielmo et al. 2011). For each bird, 3–4 measurements were taken (<12 minimum total per bird) and we used average values for statistical analyses. Repeatability of measurements was $r^2 = 0.99$ for lipid mass and $r^2 = 0.98$ for lean mass. We also estimated pectoralis muscle thickness (southern sites, $n = 24$; northern sites, $n = 82$) noninvasively (Dietz et al. 2007, Swanson and Merkord 2013, Le Pogam et al. 2020) using a LOGIQe ultrasound scanner fitted with a linear probe (12 MHz; GE Healthcare, Wauwatosa, WI). To avoid soaking the feathers with ultrasound transmission gel, we enclosed the gel (Parker Aquasonic 100) and ultrasound probe in a latex condom. We wetted the feathers of the pectoralis muscle region with water to clear the area before scanning. The probe was then placed on the bird's left pectoralis at a 90° angle to the keel, 1–2 mm from the upper keel tip. This resulted in a cross-sectional image of the muscle, where we could measure muscle thickness using a 45° angle relative to the keel. To control for potential variation due to probe position on the muscles, we also measured keel height and included it as a covariate in statistical models (Le Pogam et al. 2020). We conducted 3–4 measurements on each bird and averaged them for analyses. Repeatability of measurements was $r^2 = 0.64$ for pectoralis and $r^2 = 0.66$ for keel. All measurements were conducted by a single person (M.T.) to avoid interobserver error (Royer-Boutin et al. 2015). We then either released the birds or put them back in a cage with food and water ad libitum until metabolic measurements.

Metabolic Parameters

We used respirometry to measure thermal conductance (McNab 1980; southern sites, $n = 22$; northern sites, $n = 28$) and physiological maintenance costs via measurements of basal metabolic rate (McNab 1997, Swanson et al. 2017b; southern sites, $n = 21$; northern sites, $n = 32$). We measured conductance first during the day (mean fasting time before measurements 2.79 ± 0.34 hr). Measurement lasted 3 hr, including 2 hr for habituation to metabolic chambers, which were not considered in metabolic calculations. Birds were then kept in cages with food and water ad libitum until BMR trials overnight, which began between 18:00 and 23:00 (average: 20:20 ± 1.19 hr) and ended between 7:00 and 9:00 (average: 7:59 ± 0.59 hr) the next morning.

To measure conductance, we put birds into individual metabolic chambers (airtight 1.5 L stainless-steel containers) and exposed them to dry CO_2-free air (scrubbed with Soda lime,

Molecular Products, Louisville, CO, USA, and Drierite, 8 mesh, Hammond Drierite, Xenia, OH, USA) at a constant flow rate of 700 mL min⁻¹ controlled by mass flow controllers (Omega FMA5418A, previously calibrated with a Bubble-O-Meter, Dublin, OH, USA). The air coming out of a chamber was also scrubbed of water and CO_2 before entering one of two FoxBox oxygen analyzers (Sable Systems, Las Vegas, NV, USA). Conductance was thus measured on a maximum of 2 birds simultaneously and metabolic chambers were kept in a temperature-controlled freezer (mean temperature in chambers ($T_{chamber}$): −19.15 ± 1.05°C) for the duration of these measurements. During conductance measurements, the analyzers received scrubbed ambient "baseline" air for 10 min before and after chamber measurements which lasted 160 min, for a total of 180 min, switching between air streams using a MUX multiplexer (Sable Systems, Las Vegas, NV, USA). We recorded fractional oxygen concentration (VO_2) and temperature in the metabolic chambers with a sampling interval of 5 s. We measured body temperature (T_{body}) immediately before measurements (mean T_{body}: 41.42 ± 0.86°C) with a thermocouple reader (TC-2000, Sable Systems, Las Vegas, NV, USA) using a copper constantan thermocouple inserted ~10 mm into the cloaca and after trials as soon as the birds were taken out of their chambers (mean T_{body}: 38.33 ± 1.20°C).

A similar protocol was used for BMR measurements. The duration of trials (11.67 ± 0.18 hr) ensured a post-absorptive state for all birds (mean fasting time until reaching BMR state: 5.66 ± 2.47 hr). We measured the oxygen consumption of up to four birds at a time using two chambers per analyzer. Each analyzer received airstream from a chamber for 40 min between baselines, which lasted 10 min each, then the same sequence was repeated for the other 2 chambers. When analyzers were only monitoring one chamber each, they received airstream from the chambers for 60 min instead of 40 min. Birds received a constant flow (650 mL min⁻¹) of dry CO_2-free air and metabolic chambers were kept in a temperature-controlled cabinet maintained at 25°C (within the species' thermoneutral zone; Scholander et al. 1950) throughout trials. We used a sampling interval of 20 s to monitor VO_2 and temperature in the metabolic chambers (mean $T_{chamber}$: 24.96 ± 0.78°C).

We measured body mass before and after both trials and used the mean in conductance and BMR statistical models. Calculations for both conductance and BMR were done using ExpeData V.1.3.10 (Sable Systems, Las Vegas, NV, USA), based on the lowest averaged 10 min of the bird's oxygen consumption. Oxygen consumption was calculated using Equation 10.1 from Lighton (2019) and converted to watts using an equivalent of 19.8 kJ × L⁻¹O_2 (Gessaman and Nagy 1988). We calculated conductance (C) as

$$C = MR / \left(T_{body} - T_{ambient} \right),$$

where MR = metabolic rate (Watts), T_{body} = mean body temperature, and $T_{ambient}$ = mean ambient temperature in the chamber during the lowest 10 min VO_2.

Temperature Data

To illustrate thermal differences across our capture sites, daily mean and minimum temperatures were obtained from weather

TABLE 1. Analysis of covariance comparing structural size, wing, and tail lengths in free-living *Plectrophenax nivalis* (Snow Buntings) from the Eastern Canadian population wintering at the northern and southern sites.

Variable	Structural size			Wing length			Tail length		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
Site	0.64	1, 112	0.43	3.40	2, 111	0.07	14.60	3, 110	<0.001
Age	-	-	ns	3.77	2, 111	0.05	13.62	3, 110	<0.001
Date of measurement	-	-	ns	-	-	ns	7.14	3, 110	0.009

ns = nonsignificant, covariates that were tested but excluded from the final models because their effect was nonsignificant. To avoid confusion with the df and *F*-value of the final models, values of nonsignificant variables are represented with a hyphen (-). Models also tested for interactions between site and covariates, but these were not included in the table as they were nonsignificant. See text for details.

stations closest to capture sites (Supplementary Material Table 1) and are presented in Figure 1. Two sources were used depending on the stations: (1) Environment and Climate Change Canada (ECCC) weather office online (https://weather.gc.ca/), and (2) ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs (MELC-CFP; MELCCFP 2023).

Statistical Analysis

One of our original goals for this study was to examine potential sex effects on our parameters. However, the winter of 2023 was warm, particularly at southern sites where snowfall was minimal, and this led to very low capture success for female *P. nivalis*, with only 9 females in total (*n* = 8 in Cayuga, *n* = 1 in Fergus). We therefore removed females from statistical analyses because (1) sample sizes were strongly unbalanced (*n* = 9 for females compared to *n* = 114 for males) and (2) since females are structurally smaller, the effect of sex could not be differentiated from the effect of structural size with such unbalanced samples. Nonetheless, in the context of differential migration, female data remain important. We thus chose to visually represent females on figures, when possible, although the sex effect is not analyzed or discussed per se. Cayuga was a female-only site and was therefore not considered in analyses. As capture success for southwestern sites (Fergus, Coteau-du-Lac, and Sherbrooke) was lower and led to smaller sample sizes than northeastern sites, we combined these 3 sites and called this the "southern" site. Preliminary analyses (not shown) confirmed that measured variables did not differ among birds from those sites. Rimouski and St-Anaclet-de-Lessard are geographically close (29 km) and were also combined and called the "northern" site (see Figure 1 for the geographical locations of all sites).

To determine whether birds wintering at the northern site experienced greater physiological costs than individuals wintering in the south, we compared structural body size, body composition, plumage insulation as well as physiological maintenance costs between the two sites. Structural body size in birds is often measured as either the first axis (PC1) of a principal component analysis (PCA) combining morphological measurements, such as wing, tail, tarsus and beak lengths (Rising and Somers 1989, Freeman and Jackson 1990, Belthoff and Gauthreaux 1991, Arizaga and Bairlein 2011, Bosman et al. 2012, Petit and Vézina 2014a, Le Pogam et al. 2020), or as single trait measure, such as wing length (Nolan and Ketterson 1983, Wiklund 1996, Gosler et al. 1998, Laplante et al. 2019). However, those morphological measurements can also be considered as 2 categories: skeletal and flight feather components. Skeletal components, such as tarsus and beak lengths, represent structural measurements that vary relatively little once growth is completed. They are generally considered to reflect structural body size (Pascual and Senar 1996, Senar and Pascual 1997, Tellería et al. 2013) and are thought to be related to processes occurring during individual development (Tellería et al. 2013). In contrast, flight feather components, such as wing and tail lengths, show more short-term variability throughout the individual's life (Pascual and Senar 1996, Flinks and Salewski 2012). They are closely related to seasonal activities, changes in diet, environmental conditions, and other short-term variable effects (Harper 1994, Piersma and Drent 2003, Tellería et al. 2013). Therefore, we considered both skeletal and flight feather components separately in our site comparisons. We used the skeletal components to estimate the bird's structural size. To do so, we performed a PCA using the package *FactoMineR* (Lê et al. 2008) to combine tarsus and head + beak lengths, head + beak being less variable (CV = 2%) than beak length alone (CV = 4%). The first axis (PC1) explained the largest proportion of variance (60%) and was retained and used as our structural size variable for subsequent analysis. We initially used analyses of covariance (ANCOVAs) using the *car* package (here and below; Fox and Weisberg 2019) to compare structural size per site while considering the potential effects of bird age (second year or after second year) and date of measurement. However, since no covariates were significant, we used a *t*-test to compare structural size between sites. We also used ANCOVAs to compare flight feather components (wing and tail lengths) between sites, using structural size, age and date of measurement as covariates.

We used the same ANCOVA approach to compare total body, lean and lipid masses, as well as pectoralis muscle thickness between sites while considering the potential effects of structural size, age, and date of measurements as covariates. We further included time of measure as a covariate for total body, lean and lipid masses and keel length (see above) as a covariate for pectoralis muscle thickness. Time spent in captivity (time between capture and measure) depended on the distance between our field laboratory and capture sites and varied from one location to another (mean transportation time: 31.45 ± 53.79 min). Captivity time was thus also considered as a covariate for pectoralis muscle thickness (2.39 ± 1.45 hr), lipid mass and lean mass (1.86 ± 1.33 hr). Six individuals were removed from the pectoralis muscle thickness statistical analyses because of missing data.

We also compared conductance and BMR between sites using ANCOVA models. These models included structural size, lean mass, age, date of measurements and time spent in captivity (time between capture and the moment the bird was put
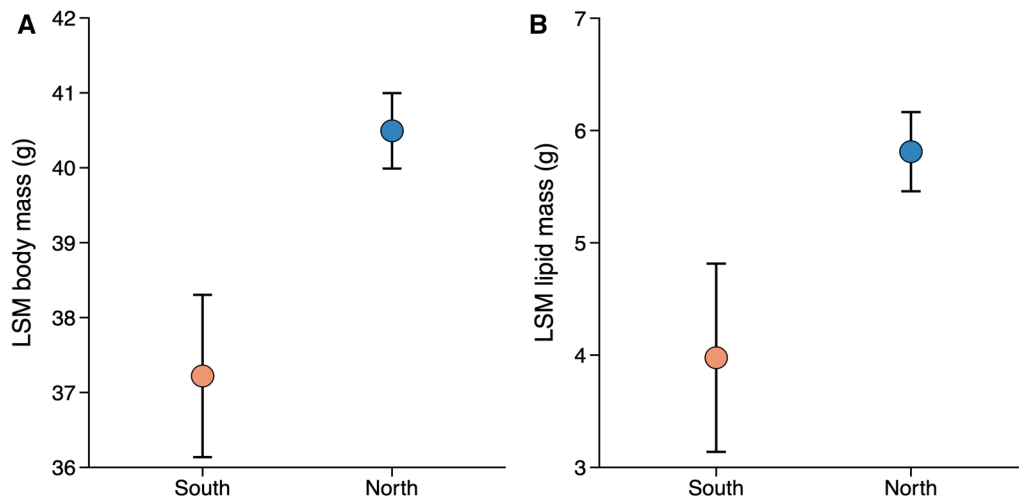
FIGURE 2. Site difference in body mass at capture (**A**) and lipid mass (**B**) in free-living *Plectrophenax nivalis* (Snow Buntings) during January and February 2023. Data are least-square means (LSM; ± SEM) by site obtained from an analysis of covariance. Covariates for each model are listed in Table 2.

in its metabolic chamber; mean time spent in captivity before conductance: 16.56 ± 13.62 hr) as covariates for conductance, while covariates for BMR included structural size, lean mass, age and time spent in captivity (mean time spent in captivity before BMR: 17.68 ± 13.88 hr). We used lean mass as a covariate rather than body mass because metabolic rates are mainly affected by non-fat components of body mass, which are more metabolically active than adipose tissues (Scott and Evans 1992). Lean mass is indeed regarded as the primary factors influencing the overall metabolic rate in birds (Piersma et al. 1996, Swanson et al. 2017a).

All models included interaction terms site*covariate, which were removed when non-significant. Repeatability of QMR and pectoralis measurements was calculated as the proportion of the overall variation attributed to variation among individuals between repeated measures (Wolak et al. 2012) using a linear mixed model with the individual as a random factor. Results per site are presented as least-square means (LSM) obtained using the package *lsmeans* (Lenth 2016) ± standard error of the mean (SEM) and therefore control for significant covariates (Packard and Boardman 1988) or as mean ± SEM. Statistical analyses were performed using R Programming Environment, 4.2.2 (R Core Team, 2022).

For all models, assumptions of normality and homoscedasticity of residuals were visually confirmed using plots of residuals against predicted values (Quinn and Keough 2002). We used an alpha threshold of 0.05 for all statistical tests.

RESULTS

Body Size

Structural body size based on skeletal structures did not differ between sites (Table 1, Supplementary Material Figure 1A, see Online Supplementary Material for a color version of this figure). Although the effect of age was only marginally significant, wing length did not differ significantly between sites; however, a trend toward longer wings in the north was observed (Table 1, Supplementary Material Figure 1B, see Online Supplementary Material for a color version of this figure). Birds wintering in the north had, on average, 2% longer tails (70.70 ± 0.29 mm) than those wintering in the south (69.50 ± 0.56 mm; Table 1,

Supplementary Material Figure 1C, see Online Supplementary Material for a color version of this figure).

Body Composition

For a given structural size, birds living in the north were, on average, 8% heavier (40.50 ± 0.25 g) than those wintering in the south (37.20 ± 0.55 g; Table 2, Figure 2A) and carried, on average, 32% more lipids in the north (5.81 ± 0.18 g) than in the south (3.98 ± 0.42 g; Table 2, Figure 2B). We also found a significant difference in lean mass between sites when considering the effects of structural size and time spent in captivity, with birds having 4% more lean mass in the north (28.20 ± 0.14 g) than in the south (27.20 ± 0.24 g; Table 2, Figure 3A). Birds wintering in the north also had thicker (1%, 68.10 ± 0.41 mm) pectoralis muscles on average than those wintering at southern sites (67.10 ± 0.86 mm; Table 3, Figure 3B).

Metabolic Parameters

Body heat loss did not differ between sites (mean conductance in the north: 0.022 ± 0.003 W °C^{-1}; in the south: 0.021 ± 0.005 W °C^{-1}; Table 3). However, we found evidences that northern birds experienced on average 8% higher maintenance costs (0.554 ± 0.009 W) compared to those living in the south (0.514 ± 0.012 W). While BMR did not vary with structural size (same analysis with structural size instead of lean mass, not shown, $P = 0.4$), it increased with lean body mass (Table 3, Figure 3C). Thus, birds carrying more metabolically active tissues also had a higher BMR (Figure 3C). However, statistically controlling for lean mass revealed that part of the maintenance cost was independent of the amount of metabolically active lean tissues present in birds. Indeed, northern birds still had a BMR 6% higher (0.550 ± 0.008 W) than *P. nivalis* wintering in the south (0.52 ± 0.01 W) when controlling for lean mass (Table 3, Figure 3D).

DISCUSSION

We studied *P. nivalis* phenotypes comparing southern and northern birds in Eastern Canada and expected to find birds wintering in the north to be structurally larger, heavier and to
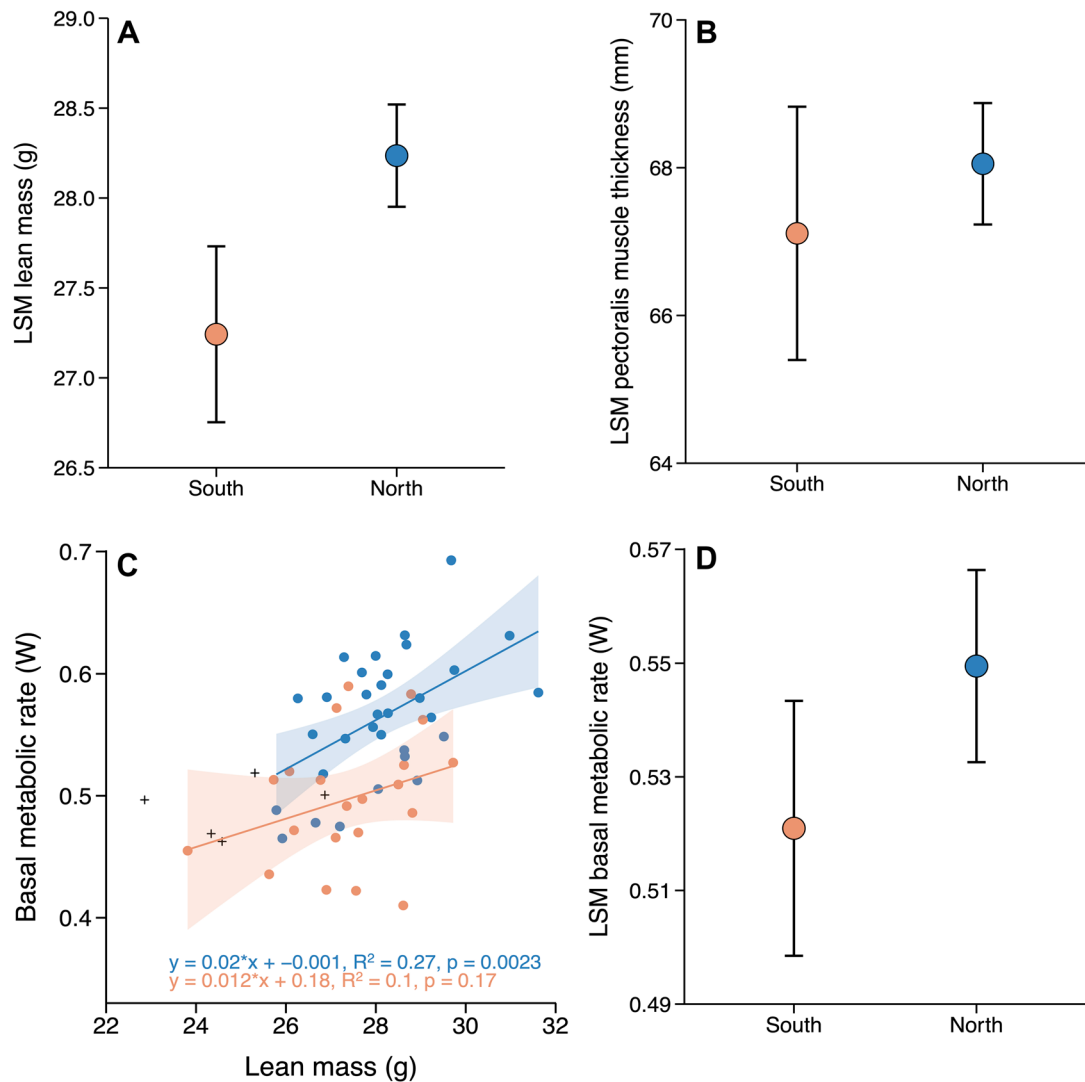
FIGURE 3. Site difference in lean mass (**A**), pectoralis muscle thickness (**B**), basal metabolic rate (**D**), and the relationship between basal metabolic rate and lean mass per site (**C**) in free-living *Plectrophenax nivalis* (Snow Buntings) during January and February 2023. Data for lean mass (**A**), pectoralis muscle thickness (**B**), and basal metabolic rate (**D**) are least-square means (LSM; ± SEM) by site obtained from an analysis of covariance. Covariates for each model are listed in Tables 2 and 3. Note that the interaction lean mass*site for basal metabolic rate is not significant but is presented to visualize the site effect (**C**). Females were not included in analyses but are visually represented with crosses for basal metabolic rate (**C**). Individuals wintering in the northern site are represented in blue while individuals wintering in the southern sites are represented in orange.

carry more lipid stores and have more lean tissues. We also expected birds at northern sites to have larger pectoralis muscles, better feather insulation, and higher maintenance costs. We found that birds had similar structural size and body heat loss across sites. Nevertheless, birds wintering in the north were 8% heavier and carried, on average, 32% more lipids than *P. nivalis* wintering in the south. They also had longer tails and tended to have longer wings. Northern birds further maintained thicker pectoralis muscles, had 4% more lean tissues, and experienced 8% higher maintenance costs on average, costs that were still 6% higher after statistically controlling for the effect of metabolically active lean tissue mass. Although based on a single winter of data, these results suggest that *P. nivalis* wintering farther north pays a significant and measurable cost of wintering in the cold possibly to gain the expected fitness advantage of shorter spring migration distances to their Arctic breeding grounds.

Morphological Traits and Body Composition

Our findings indicate that *P. nivalis* wintering in colder and harsher northern regions (Laplante et al. 2019) are not structurally larger but do have longer tails and marginally longer wings. These results are comparable to those of previous studies on the same Canadian population showing that *P. nivalis* wintering in cold and snowy sites have longer wings than individuals spending the winter in milder conditions (Macdonald et al. 2016, Mckinnon et al. 2019). Other studies have also reported larger birds at cold northern winter sites but, although they often incorporated wing and/or tail length in their size calculation (e.g., Prescott 1994, DeVries et al. 2022) or relied solely on wing length for sizing estimations (e.g., James 1970, Ashton 2002, Romano et al. 2020), those studies typically did not make the distinction between skeletal and flight feather metrics of body size. Longer wings are thought to improve flight efficiency in some cases (Roeder et al. 2019,

TABLE 2. Analysis of covariance (ANCOVA) comparing body, lipid, and lean masses in free-living *Plectrophenax nivalis* (Snow Buntings) from the Eastern Canadian population wintering at the northern and southern sites.

Variable	Body mass at capture			Lipid mass			Lean mass		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
Site	68.33	4, 109	<0.001	92.17	3, 110	<0.001	10.51	3, 110	0.002
Age	-	-	ns	-	-	ns	-	-	ns
Structural size	5.53	4, 109	0.02	-	-	Ns	3.87	3, 110	0.05
Date of measurement	3.59	4, 109	0.06	24.04	3, 110	<0.001	-	-	ns
Time of measurement	5.01	4, 109	0.03	-	-	ns	-	-	ns
Time spent in captivity				7.15	3, 110	0.009	10.03	3, 110	0.002

ns = nonsignificant, covariates that were tested but excluded from the final models because their effect was nonsignificant. To avoid confusion with the df and *F*-value of the final models, values of nonsignificant variables are represented with a hyphen (-). Variables that were not included as covariates in the initial model are represented with an empty cell. Models also tested for interactions between site and covariates but these were not included in the table as they were nonsignificant. See text for details.

TABLE 3. Analysis of covariance (ANCOVA) models comparing pectoralis muscles thickness, conductance, and basal metabolic rate in free-living *Plectrophenax nivalis* (Snow Buntings) from the Eastern Canadian population wintering at the northern and southern sites.

Variable	Pectoralis muscle thickness			Conductance			Basal metabolic rate		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
Site	142.51	6, 93	<0.001	0.32	2, 47	0.57	30.40	3, 48	<0.001
Age	14.49	6, 93	<0.001	-	-	ns	-	-	ns
Structural size				-	-	ns	-	-	ns
Body mass at capture	47.57	6, 93	<0.001						
Date of measurement	58.22	6, 93	<0.001	-	-	ns			
Time spent in captivity	19.47	6, 93	<0.001	10.64	2, 47	0.002	11.08	3, 48	0.002
Keel length	191.94	6, 93	<0.001						
Lean mass				-	-	ns	13.93	3, 48	<0.001

ns = nonsignificant, covariates that were tested but excluded from the final models because their effect was nonsignificant. To avoid confusion with the df and *F*-value of the final models, values of nonsignificant variables are represented with a hyphen (-). Variables that were not included as covariates in the initial model are represented with an empty cell. Models also tested for interactions between site and covariates, but these were not included in the table as they were nonsignificant. See text for details.

Ydenberg et al. 2023) and, in species using bounding flight, longer tails are thought to enhance lift and stability (Sachs and Lenz 2011, Roeder et al. 2019). While *P. nivalis* were structurally comparable between sites, northern individuals were nevertheless 8% heavier and carried 32% more lipids on average than those wintering in the south. It thus appears that individuals with longer wings and tails in the north could have been advantaged to carry their heavier weight (Norberg 1995, Swaddle et al. 1996). This also corroborates earlier observations in *P. nivalis* where larger males, characterized by longer wings, winter north relative to smaller females (Macdonald et al. 2016).

Plectrophenax nivalis are considered nomadic birds in winter (Macdonald et al. 2012, Simard-Provençal 2024), with cumulative movements averaging 121 ± 46 km from December to February (Mckinnon et al. 2019) likely in response to locally reduced food access due to snow cover (Laplante et al. 2019). However, they can also winter at very distant locations among years. For example, an individual wintering in Western Europe one winter was found in North America the next (Banks et al.

1991). It is not clear at the moment what may drive the choice of specific wintering sites. For example, site choice could be partly driven by the capacity of birds to carry a heavier body (e.g., flight feather length). However, constraints during molt can affect feather quality and flight feather length (Pehrsson 1987, Murphy et al. 1988, Pap et al. 2008) while wear and tear of plumage can lead to a loss of flight performance (Swaddle et al. 1996, Hedenström 2023). Given that life at colder and harsher northern sites likely requires more lipid stores (this study), it is reasonable to assume that *P. nivalis* might be forced to winter farther south to reduce flight costs and loss of maneuverability on years when wings and tails are shorter (Norberg 1995, Tellería et al. 2001). This would suggest that conditions during molt in the Arctic could have far-reaching downstream effects on wintering costs and location, although this requires further studies.

The observed 32% greater lipid reserves in birds at northern sites is most likely a response to cold and unpredictable wintering conditions in the north (Laplante et al. 2019). Indeed, outdoor captive *P. nivalis* kept in the same area as our northern

sites have been shown to increase their lipid mass by 246% during the fall transition toward winter (August to October) and to maintain these large lipid stores throughout the winter (Le Pogam et al. 2020). Laplante et al. (2019) further showed that snow depth and temperature are important predictors of lipid storage in free-living *P. nivalis* with birds carrying larger lipid stores on colder and snowier days. Lipids are the prime metabolic fuel for small avian species during winter (Blem 1976, Dawson et al. 1983). Storing lipids not only helps birds endure prolonged cold nocturnal fasts but also prepares them to cope with unpredictable food availability (Blem 1976, Lehikoinen 1987, Marsh and Dawson 1989, O'Connor 1995, Gosler 1996). Our data thus support the prediction that *P. nivalis* wintering closer to their breeding grounds are required to carry larger amounts of lipids to face colder and snowier winters, shorter day lengths and likely more unpredictable conditions than their southern counterparts.

Living in the cold typically leads to a gain in lean mass for birds (Dawson and Marsh 1986, Petit et al. 2014), including in captive *P. nivalis* (Le Pogam et al. 2020), a pattern that aligns with our observations, as northern birds exhibited 4% higher lean mass (Figure 3A). This is often explained by an increase in the size of several internal organs such as nutritional and cardiopulmonary organs (Zheng et al. 2008, Liknes and Swanson 2011, Swanson and Merkord 2013, Barceló et al. 2017), as well as pectoralis muscles (O'Connor 1995, Cooper 2002). Our data also revealed that pectoralis muscle thickness was greater in the north and increased with total body mass in *P. nivalis*, a relationship also observed in other avian species (Marsh and Storer 1981, Marsh 1984, Lindström et al. 2000, Vézina et al. 2006b). Therefore, while thicker pectoralis muscles could be advantageous for shivering heat production in the north (O'Connor 1995, Cooper 2002, Petit and Vézina 2014a, Swanson et al. 2017a, Milbergue et al. 2018), it likely also supports flight with a heavier body (Marsh and Storer 1981, Marsh 1984, Lindström et al. 2000, Dietz et al. 2007) and higher wing-loading (Marsh and Storer 1981, Fry et al. 1972).

Metabolic Parameters

Body heat loss, measured as thermal conductance, did not differ significantly between birds wintering at the northern and southern sites. Therefore, it appears that *P. nivalis* wintering at northern, colder sites do not benefit from better insulation. Our conductance values (0.022W °C⁻¹) at the northern sites are comparable to those reported by Demers et al. (2023) (~0.025W °C⁻¹) for the same location in *P. nivalis*. However, Demers et al. (2023) also reported a 12% greater heat loss in adult birds relative to juveniles experiencing their first winter of life, a difference that was not detected in our study. This inconsistency most likely results from differences in sampling protocols and variability among years as Demers et al. (2023) used data collected over three years ($n = 189$, including 102 first-year birds) while the current study was conducted in a single winter ($n = 28$ at the northern sites, including 10 first-year birds).

Our data also revealed that birds wintering at northern sites experienced 8% higher maintenance costs, measured as BMR (McKechnie et al. 2015, Swanson et al. 2017b). Elevated BMR is commonly reported during the cold season in birds experiencing seasonal environments (Broggi et al. 2007, Zheng et al. 2014, Broggi et al. 2019). It is also observed at colder northern

latitudes (Piersma et al. 1996, Broggi et al. 2007, Wiersma et al. 2007, Zheng et al. 2014, Broggi et al. 2019) and in captive birds maintained in cold experimental conditions (Vézina et al. 2006a, Barceló et al. 2017, but see Le Pogam et al. 2020, see McKechnie 2008, McKechnie et al. 2015, Swanson et al. 2022 for reviews).

Changes in maintenance costs are typically associated with phenotypic adjustments in several physiological traits. For example, Petit et al. (2014) reported a 6% seasonal increase in BMR in wintering *Poecile atricapillus* (Black-capped Chickadee) compared to the summer phenotype, a difference similar to the one reported here. Although seemingly modest, this increase in metabolic rate was nevertheless associated with major changes in body composition, including the enlargement of highly active organs such as flight muscles, the heart, kidneys and intestines (Petit et al. 2014), changes that are in direct response to experienced environmental constraints. For example, as cold exposure leads to higher rates of daily food intake (McWilliams et al. 1999, Williams and Tieleman 2000, Vézina et al. 2006a), cold acclimation and acclimatization are typically associated with enlarged digestive and excretory organs (Williams and Tieleman 2000, Zheng et al. 2008, Petit et al. 2014, Barceló et al. 2017), which contribute to increased BMR (Williams and Tieleman 2000, Li et al. 2011, Petit et al. 2014, Barceló et al. 2017). Latitude effects have also been reported on maintenance costs for other non-migrant species. For instance, Broggi et al. (2007) compared two populations of *Parus major* (Great Tit) wintering at different latitudes (Lund: 55°40'N, 13°25'E and Oulu: 65°00'N, 25°30'E) in Sweden over 6 consecutive winters and reported consistently higher BMR in birds of the northern population.

Lean mass had a clear influence on maintenance costs in *P. nivalis* (Figure 3C), but our data also show that BMR was not solely driven by the amount of metabolically active tissues. Indeed, the site effect remained significant after statistically controlling for lean mass, with birds wintering in the north still experiencing a 6% higher BMR. In other words, basal metabolic rate was also higher per unit of lean tissue mass in northern wintering birds, indicating an upregulation of metabolic intensity in individuals facing harsher conditions. Metabolic intensity is typically attributed to the cellular metabolism of vital tissues (Swanson and Olmstead 1999, Broggi et al. 2007, Zheng et al. 2008, Petit and Vézina 2014b, Swanson et al. 2017b). Collectively, these results thus support the hypothesis that *P. nivalis* experience high maintenance cost, and to a certain degree, disproportionately high maintenance cost per unit lean mass, when wintering at northern sites.

Conclusions

Plectrophenax nivalis from the Eastern Canadian population exhibit differential distribution on their wintering grounds, leading individuals at different latitudes to experience diverse winter conditions. Birds wintering at northern sites may benefit from early arrival on their Arctic breeding grounds and higher reproductive success (Guindre-Parker et al. 2013), but wintering closer to their breeding habitat could also come with the cost of supporting the physiological machinery required to survive in these conditions. Indeed, wintering birds measured at our northern sites were heavier, carried more body lipids, had higher amounts of lean tissues and experienced higher

physiological maintenance costs, likely driven in part by larger internal organs associated with life in the cold (Williams and Tieleman 2000, Li et al. 2011, Barceló et al. 2017). Birds caught in the north also had larger flight muscles, which help flying with a heavier body (Pennycuick 1975, Marsh and Storer 1981, Marsh 1984, Lindström et al. 2000, Dietz et al. 2007) and produce heat during shivering (Marsh and Dawson 1989, Swanson 2010). While our study exclusively focused on male *P. nivalis*, future investigations should compare wintering physiology in both males and females, the latter having recently been found to carry a disproportionate amount of lipids compared to males (Laplante et al. 2019), possibly highlighting different demands and constraints between sexes during the cold season.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

All bird handling and measurements were approved by the animal care committee of the Université du Québec à Rimouski (CPA-92-22-250) and were conducted under scientific (SC-48) and banding (10511, 10622, 10622F, 10752, 10889, 10892B) permits from Environment and Climate Change Canada.

Conflict of interest statement

The authors have no competing interests.

Author contributions

M.T., A.L.P., F.V., and O.P.L. conceived the ideas and designed methodology; M.T. collected and analyzed the data; M.T., A.L.P., F.V., and O.P.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

Analyses reported in this article can be reproduced using the data provided by Turcotte et al. (2025).

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