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RESEARCH ARTICLE

Coping with the worst of both worlds: Phenotypic adjustments for cold acclimatization benefit northward migration and arrival in the cold in an Arctic-breeding songbird

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Abstract

- Cold acclimatization (phenotypic adjustments to cope with cold conditions) is an imperative requirement for birds living at high latitudes during the cold depths of winter. Despite the significant remodelling of key phenotypic traits and energetic costs associated with elevating cold endurance, winter cold acclimatization can also provide further carryover benefits to subsequent stages in species wintering, migrating and breeding in cold environments (e.g. the Arctic).
- 2. We tested this beneficial carryover hypothesis using outdoor captive Arcticbreeding snow buntings *Plectrophenax nivalis*, a cold specialist known for its impressive wintering thermogenic capabilities. We compared changes in phenotypic traits supporting cold acclimatization—body composition (body, fat, lean mass, pectoral muscle thickness), oxygen carrying capacity (haematocrit), thermogenic capacity and endurance (M_{sum} , time to M_{sum}), cold tolerance (T_a at M_{sum}) and maintenance energy expenditure (BMR)—between the wintering, migratory and arrival/summer stages.
- 3. Body mass (+31%), fat mass (+226%) and BMR (+13%) increased relative to the winter phenotype, likely to support the added costs of migration—that is the *migratory upregulation hypothesis*. In contrast, lean mass, pectoral muscle thickness, haematocrit and thermogenic capacity remained high and stable at winter level across stages in support of the *thermal carryover hypothesis*. The maintenance of these traits likely offers spare capacity for unpredictable cold environments expected during migration and breeding in the Arctic.
- 4. Our results thus suggest that birds can extend the long-term advantages of winter phenotypic adjustments through additional benefits to thermogenic capacity during subsequent life-history stages. These benefits likely make it possible for Arctic-breeding birds to maximize success across diverse life-history stages in the face of extreme cold conditions.

KEYWORDS

Arctic bird, BMR, body composition, carryover, cold acclimatization, fattening, migration, $M_{\rm sum}$

1 | INTRODUCTION

Organisms often face trade-offs within and across life-history stages, wherein they must allocate time and resources towards phenotypic adjustments that are best suited for current environmental demands, while avoiding negative long-term effects onto future stages (Harrison et al., 2011). For temperate bird species, two life-history stages that are particularly energetically demanding, and require significant phenotypic adjustments, are wintering in the cold (Cooper & Swanson, 1994; Dawson et al., 1983; Petit et al., 2013) and subsequent migration (Alerstam & Lindström, 1990; Berthold et al., 2003; Blem, 1980). Although these two stages are often viewed as mutually exclusive, birds can exhibit similar trait adjustments in support of these highly active phenotypes. First, both depend on substantial aerobic endurance (Dawson et al., 1983), higher oxygen carrying capacities (Chilgren & DeGraw, 1977; Krause et al., 2016) associated with developed cardiopulmonary organs and flight muscles (e.g. Battley & Piersma, 1997; Dietz et al., 2007; Liknes & Swanson, 2011; Petit et al., 2014; Piersma et al., 1999), as well as increases in maximal shivering heat production during cold acclimatization (i.e. summit metabolic rate, $M_{\rm sum}$; Swanson et al., 2013; Petit & Vézina, 2014; Petit et al., 2017) and peak effort endurance for migration (i.e. maximum metabolic rate, MMR; Chappell et al., 1999; Klaassen et al., 2000; Piersma, 2011). Second, both stages are characterized by periods of positive energy budget that enable the accumulation of fat stores as the main source of fuel for prolonged shivering and long-distance flights (Dawson et al., 1983). This accumulation of stores can lead to an increase in the mass of nutritional organs (e.g. Barceló et al., 2017; Petit et al., 2014; Piersma et al., 1999; Swanson, 1991a), allowing for better assimilation of nutrients (Bairlein, 1985) and greater supply of metabolizable energy. Lastly, both stages exhibit considerable protein accumulation and increase in lean mass (e.g. Chaplin, 1974; Dawson & Marsh, 1986; Lindström & Piersma, 1993; Petit et al., 2014; Piersma, 1990) which can increase the overall energy consumption of resting birds, thereby increasing physiological maintenance costs (i.e. basal metabolic rate-BMR, McKechnie et al., 2015; Swanson & Dean, 1999; Swanson, McKechnie, et al., 2017).

Given the similar phenotypic adjustments involved in cold acclimatization and preparation for migration, some studies have examined the potential benefits of one life-history stage carrying over to the other. For example, because prolonged shivering and long-distance flight share muscle function (Marsh & Dawson, 1989; Wiersma et al., 2007), investigations have found that muscle preparation for spring migration also improves M_{sum} (Corder & Schaeffer, 2015; Swanson, 1995; Swanson & Dean, 1999; Vézina et al., 2007). However, most studies have focused on neotropical or mild-temperate passerines (e.g. Swanson, 1995; Swanson & Dean, 1999), and although an elevated thermogenic capacity in the spring may occur as a byproduct of flight endurance adaptations (Zhang et al., 2015), any benefits gained from phenotypic changes for migration may not fully advantage species that do not face constraining cold conditions. In contrast, in temperate species that encounter cold temperatures in the spring when migrating towards higher latitudes and even when arriving early on their breeding grounds, the increase in $M_{\rm sum}$ as a by-product of flight endurance adjustments may be a clear performance benefit in the cold at subsequent life-history stages (Vézina et al., 2007). In addition, experimental cold-training (short daily exposures to cold) can also lead to better exercise endurance in birds (Zhang et al., 2015). While this suggests that winter cold acclimatization could be advantageous for migration in species that depart early enough in the spring to still be expressing high cold hardiness, this hypothesis has never been tested.

We used the Arctic-breeding snow bunting Plectrophenax nivalis, a 30-50 g songbird known for its winter cold endurance (Le Pogam et al., 2020; Scholander et al., 1950) and early spring departure (McKinnon et al., 2019; Snell et al., 2018) to determine whether a winter cold-associated phenotype can be maintained to provide thermoregulatory benefits for migration towards and arrival on cold. high latitude breeding grounds. Snow buntings require significant phenotypic adjustments to winter in the open, snowy and cold conditions (Le Pogam et al., 2020) of North America, Europe and Asia. In spring, these birds migrate through winter landscapes well before snow melt (Macdonald et al., 2012; McKinnon et al., 2016). Males arrive on the breeding grounds (up to latitudes of 83.6°N) in late April to secure territories and up to 1 month before females (Cramp & Perrins, 1994; Montgomerie & Lyon, 2011; Snell et al., 2018). During this period, conditions can be comparable or worse than those during winter with extensive snow cover and air temperatures (T_{a}) reaching -30°C (Meltofte, 1983). Since buntings are already cold acclimatized when they enter the spring migratory period (Le Pogam et al., 2020), they are an ideal species for investigating whether phenotypic adjustments for winter are maintained to provide thermoregulatory benefits for migration and arrival in the cold. Using an outdoor captive population, we tracked phenotypic changes in traits underlying cold acclimatization and migration, namely body composition (total body mass (M_b), fat and lean mass and pectoral muscle thickness), oxygen carrying capacity (haematocrit), maximum thermogenic capacity (M_{sum}), thermogenic endurance (time to M_{sum}), cold tolerance $(T_{a} \text{ at } M_{sum})$ and maintenance energy expenditure (BMR), from the period of migratory preparation, to when birds would arrive on the breeding grounds and then until the end of summer.

We formulated two hypotheses to predict potential outcomes given the species' life history. First, buntings could exhibit a phenotypic pattern typical of most migratory birds by increasing body composition parameters (i.e. total M_b , fat mass and lean mass) and oxygen carrying capacity, relative to the winter period to support flight and arrival costs (e.g. Western sandpiper *Calidris mauri* Guglielmo & Williams, 2003; Gambel's white-crowned sparrows *Zonotrichia leucophrys gambelii* Krause et al., 2016). These changes could generate concomitant increases in BMR and M_{sum} relative to the winter period (Vézina et al., 2007). We termed this the *migratory upregulation hypothesis*. Under this hypothesis, phenotypic adjustments made for migration would provide additional capacity for coping with cold during migration and arrival on the Arctic-breeding grounds. Studies have already provided support for this hypothesis (Corder & Schaeffer, 2015; Swanson, 1995; Swanson & Dean, 1999), although only one examined an Arctic-breeding species (red knot *Calidris canutus* Vézina et al., 2007). Alternatively, buntings could benefit from cold acclimatization adjustments made before migration, a second hypothesis that we termed the *thermal carryover hypothesis*. Under this previously unstudied scenario, the winter phenotype would be maintained into the spring as it would be sufficient to provide both cold and flight endurance for migration. Thus, except for fat stores and total M_b (Vincent & Bédard, 1976), we would predict no increase in body composition parameters, oxygen carrying capacity and M_{sum} , contrary to what is typically observed in other migratory birds. Basal metabolic rate, which depends largely on metabolically active lean tissues (Piersma, Bruinzeel, et al., 1996; Piersma et al., 2004; Swanson, King, et al., 2017), would also remain stable relative to the winter period.

2 | MATERIALS AND METHODS

2.1 | Captive housing conditions

This study covers the period between March and August of each year, from 2014 to 2018, during which we studied captive male snow buntings at the avian facilities at the Université du Québec à Rimouski, Canada (48°27'00"N; 68°30'45"W). This work also includes data collected in December (shortest days), January and February (coldest days) for direct comparisons to an established winter phenotype (see Le Pogam et al., 2020 for a full analysis of winter phenotypic variation in snow buntings). Birds were maintained in an outdoor aviary previously described by Le Pogam et al. (2020) after being captured in open fields around Rimouski between January and March of each year using walk-in traps baited with cracked corn. Birds were banded at capture with a unique combination of four colour bands for individual identification. Additionally, we collected morphometric measurements (length of head plus beak, tarsus, tail, right wing) at capture to calculate a 'structural body size index' (details below). Once in the aviary, birds were fed ad libitum with a commercial seed mix (crushed corn, wheat, sorghum, white millet, red millet, black oil sunflower; Armstrong) and Mazuri Small Bird Maintenance Mini Diet (#562A; Mazuri). We also provided ice-free water ad libitum supplemented with electrolytes (0.17 g/L; Electrolytes Plus, Vetoquinol N.-A. Inc.) and vitamins (0.44 g/L; Poly-tonine A Complex, Vetoquinol N.-A. Inc.). The size of our study group varied between 16 and 44 birds (migration and summer only, average group size over the 5 years = 25.9 ± 0.9 males) and totalled 120 individual birds due to the addition of new individuals each winter to replace mortalities and individuals removed for other experiments.

2.2 | Air temperature measurements

Air temperature was measured in the aviary using a temperaturesensitive data logger (iButton DS1922L, Maxim Integrated) suspended 1.5 m above the ground in the shade. Air temperature was recorded every 10 min and we calculated daily average, minimum and maximum T_a . Missing data (11.6% of total dataset for this period) were obtained from regressions between iButton T_a data and T_a data extracted from the nearest weather station (48°30′50″N; 68°28′06″W, Government of Canada http://climat.meteo.gc.ca; average daily $T_a r^2 = 0.98$; min $T_a r^2 = 0.97$; max $T_a r^2 = 0.97$).

2.3 | Experimental design and sampling sequence

Although our birds could not migrate, this study covers the transition between wintering and migratory phenotypes (March-May; Macdonald et al., 2012; McKinnon et al., 2019; Vincent & Bédard, 1976) and extends to the end of summer (early August). Birds did not breed in captivity but did undergo their postnuptial moult (starting in July). Each captive bird was repeatedly measured over the study period (range: 1-49 times, average: 11 times, depending on individuals and up to 69 times including winter data, see Table S1). Metabolic performance (M_{sum} and BMR), haematocrit and pectoral muscle thickness were only measured in 2015 (Table S1). Experimental trials measuring metabolic performance, haematocrit and body composition on the same day were limited to four birds per day, resulting in an average of 11.5 days to measure all birds. Experimental trials that did not include metabolic performance were carried out on all birds in 1 day. Each trial for a given month was conducted on similar dates each year (see Table S1).

2.4 | Haematocrit and body composition measurements

We captured birds in the aviary between 08:00 and 11:30 using a hand-held net. At capture, a blood sample (<1% of total $M_{\rm b}$) was immediately collected from the brachial vein. Blood samples were temporarily stored in a refrigerator and later centrifuged for 10 min at 6,595 g (UNICO PowerSpin BX Centrifuge C886) to obtain haematocrit data and plasma samples for parallel studies. We then weighed $(\pm 0.01 \text{ g})$ all birds and we non-invasively estimated the fat and lean component of their $M_{\rm b}$ using a quantitative magnetic resonance (QMR) apparatus (±0.01 g; EchoMRI; Guglielmo et al., 2011). We took three to four QMR measurements for each bird (<12 min total), and the average value was subsequently used for analyses. We then measured pectoral muscle thickness by ultrasonography (Dietz et al., 2007; Swanson & Merkord, 2013) following Le Pogam et al. (2020) using a LOGIQe ultrasound scanner fitted with a linear probe (12 MHz, GE Healthcare). Three to four measurements of pectoral muscle thickness and keel height were obtained for each bird and average values were used in analyses (repeatability of ultrasound measurements: r = 67% for pectoral and r = 69% for keel; but see Royer-Boutin et al., 2015). Birds were then moved to an indoor cage (117 cm W \times 39 cm H \times 310 cm D) with food and water provided ad libitum until release into the aviary or metabolic performance measurements.

2.5 | Metabolic performance measurements

Metabolic rates were measured using the instruments and protocol described in detail by Le Pogam et al. (2020), which are briefly presented here. Summit metabolic rate was measured on two birds simultaneously, allowing for two trials per day. Birds were taken from their cages at least 1 hr after ultrasound measurements for the first M_{sum} trial. At this point, their feathers were completely dry [our technique does not involve contact with ultrasonography gel, see Le Pogam et al. (2020); Royer-Boutin et al. (2015)]. First trials started between 11:00 and 16:30 (average: 13:19 \pm 0.95 hr; duration: 1.92 \pm 0.8 hr) and second trials between 13:00 and 18:00 (average: $15:42 \pm 1.18$ hr; duration: 1.70 ± 0.7 hr). Each trial began by measuring a bird's $M_{\rm h}$ and body temperature ($T_{\rm b}$: type-T thermocouple ~10 mm into the cloaca, mean $T_{\rm b}$ before $M_{sum} = 40.8 \pm 0.8$ °C). Birds were then placed inside metabolic chambers (1.5 L) equipped with a perch and a type-T thermocouple to monitor chamber T_{a} , which were kept in a temperature-controlled cabinet. Birds were first exposed to dry, $\rm CO_2$ -free air for 10 min at -18°C (-15°C in August). Chamber inflow was then switched to a helox gas mixture (1,200 ml/min, 21% oxygen, 79% helium, Rosenmann & Morrison, 1974). A 5-min baseline in helox at -18°C or -15°C was recorded before measuring the birds' oxygen consumption. Chamber temperature was lowered by 3°C every 20 min until birds became hypothermic (i.e. a visible steady decline of $\dot{V}O_2$ for several minutes) or reached the end of the program. Birds with a $T_{\rm b}$ < 37°C at the end of a trial were considered hypothermic (Swanson & Liknes, 2006). Thirteen measurements out of 225 (5.8%) involved birds that were not hypothermic ($T_{\rm b} \ge 37^{\circ}$ C) at the end. However, since a hypothermic state is not a prerequisite to confirm M_{sum} (Dutenhoffer & Swanson, 1996), we opted to include these individuals in final analyses (removing them had no influence on results). As chamber temperature changed automatically every 20 min during M_{sum} trials, birds experienced the same measurement sequence. This allowed for the calculation of individual thermogenic endurance (sensu Swanson & Liknes, 2006), defined here as the time needed to reach $M_{\rm sum}$ (hereafter, time to $M_{\rm sum}$). We also extracted the chamber T_a at which each bird attained their M_{sum} (hereafter, T_a at M_{sum}). Birds were then placed back in their cage and given food and water until BMR measurements.

Basal metabolic rates were measured overnight on four birds simultaneously. Birds were given at least 1 hr of rest between $M_{\rm sum}$ and BMR measurements. Hence, BMR measurements began between 17:00 and 22:00 (average: 19:04 ± 1.10 hr) and ended between 07:10 and 9:20 (average: 7:55 ± 0.52 hr) the next morning. Birds were placed in metabolic chambers kept at 25°C, a temperature within the thermoneutral zone for this species (Scholander et al., 1950), and received dry CO₂-free air at 650 ml/min. Air was then sampled, alternating between a baseline channel for 10 min and chamber channels for 40 min. After BMR measurements, birds were released back to the aviary.

Temperatures in chambers and \dot{VO}_2 were recorded every 5 s for M_{sum} and every 20 s for BMR. Summit metabolism and BMR were calculated from the highest and lowest averaged 10 min of \dot{VO}_2 , respectively, using equation 10.1 from Lighton (2019). Summit

metabolism calculation included an instantaneous transformation (Bartholomew et al., 1981). Shivering uses fat as fuel (Vaillancourt et al., 2005) and duration of BMR trials (around 12.33 \pm 1.19 hr) insured that birds were post-absorptive at the time of BMR measurement (which occurred after 4.36 \pm 2.19 hr of measurement). We therefore estimated energy expenditure for all measurements using an equivalent of 19.8 kJ/LO₂ and converted units to Watts (Gessaman & Nagy, 1988).

2.6 | Moult intensity and timing

Since feather moult may influence lean body mass (Silverin et al., 1999; Walsberg & King, 1978) we examined the timing and intensity of moult with regard to changes in lean mass. Moult intensity was scored from June to August in 2018 (see Table S1) in two areas of the body: tail and wings (primary feathers). Each feather was attributed a score between 0 and 5 for a maximum score of 60 for the tail and 50 for each wing (160 in total). The following scores were used: 0—no moult (old feather); 1—pin only; 2—small feather; 3—half length; 4—3/4 length and 5—growth complete (new feather). To obtain an estimate of the individual rate of moult, we calculated the difference between two individual scores measured at least 2 weeks apart and divided it by the number of days separating them (average 15.25 days, range 12–28 days). These scores, therefore, represent the daily change in moult score in normal scaling units per day (hereafter 'moult intensity').

2.7 | Statistical analysis

We used linear mixed-effects models to analyse temporal patterns of variation for each parameter. We included 'Bird ID' as a random variable in all models to control for repeated measurements on the same birds. Models included 'month' as a categorical variable, corresponding to the sequence of measurement including one or more measures per month (e.g. March-1, March-2, etc.; Table S1). However, for parameters measured only in 2015, winter data included values only for that year. The variable 'year' was ultimately treated as a random variable because we were not focused on 'year effects' per se (but rather wished to control for this degree of variation), and since we did not have measurements for all months in each of the 5 years. To represent inter-annual variation for each parameter visually, we conducted the same linear mixed-effects models for each year separately and generated the least square means per year presented in the figures. Although our captures were all conducted in the morning, we considered the potential effect of daily fattening (e.g. Laplante et al., 2019) on our variables by also including 'relative time of capture' in the models (calculated as the time between sunrise and capture/day length). We also initially included day length in our models to take into account the effect of photoperiod. However, as this variable was not found to be significant, it was not included in subsequent models. We further included a measure of 'structural

body size' as a covariate in our models to control for the influence of size on $M_{\rm b}$ lean and fat mass, and on muscle thickness. Since they control for all independent variables and covariates, least square means resulting from models with a significant body size effect are considered 'size-independent'. This 'structural body size' estimate was the first principal component obtained from a principal component analysis combining variation in the lengths of head plus beak, tarsus, wing and tail (Rising & Somers, 1989). For analyses investigating variation in muscle thickness, we also included 'keel height' as a covariate to control for variation in thickness due to ultrasound probe positioning (see Le Pogam et al., 2020). Variation in metabolic performance was first analysed considering whole-animal M_{sum} , time to M_{sum} , T_{a} at M_{sum} and BMR. Then, because changes in the amount and activity of lean tissue are considered the main driver of wholeanimal metabolic rate in birds (Piersma, Bruinzeel, et al., 1996; Piersma et al., 2004; Swanson, King, et al., 2017), we included lean mass as a covariate in those models to examine 'mass-independent' variation. Under scenarios when whole and mass-independent results were similar, mass-independent values are presented. Note that individuals starting at -15° C during M_{sum} measurements were removed from analyses on time to M_{sum} .

In addition to the above analyses, we also investigated how total $M_{\rm b}$ varied in relation to fat mass across the sampled period (excluding winter). We thus extracted least square means generated by our mixed-effects models (controlling for structural body size and time of capture with year and bird ID as random parameters), and used them in a linear regression where each point then represented an average value for a specific time point (see Le Pogam et al., 2020; Vézina et al., 2011). Therefore, this 'new' dataset included 21 values for each parameter. We used the same approach to investigate how $M_{\rm sum}$ (whole and controlled for lean mass) varied in relation to pectoral muscle thickness and haematocrit (in 2015) and how lean mass (controlled for structural body size) varied in relation to moult intensity from July to October 2018 (adding September and October to the dataset for this specific analysis, see results). These 'new' datasets included 10, 11 and 7 values respectively.

Visual inspection of residuals confirmed assumptions of normality and homogeneity for all models. Analyses were conducted using JMP pro (14.0.0) and data are presented as mean \pm standard error of the mean (*SEM*) in the text and 95% confidence intervals (CI) in graphs. Post-hoc contrasts were used to determine differences between selected months.

3 | RESULTS

3.1 | Air temperature

Air temperatures were regularly below 0°C in March (mean $T_a = -4.4 \pm 0.3$ °C, mean max $T_a = -0.3 \pm 0.4$ °C, mean min $T_a = -8.5 \pm 0.3$ °C; Figure 1) and gradually increased from April until peaking in July-August (mean $T_a = 20.3 \pm 0.2$ °C, mean max $T_a = 25.0 \pm 0.3$ °C, mean min $T_a = 15.9 \pm 0.1$ °C; Figure 1).



FIGURE 1 Variation in mean, minimum and maximum air temperatures experienced by outdoor captive snow buntings in Rimouski, Québec, Canada from 2014 to 2018

3.2 | Body composition and oxygen carrying capacity

Controlling for the effect of structural size ($F_{1,103} = 9.0, p < 0.05$), M_b varied with time (month: $F_{26,1.493} = 114.5, p < 0.0001$, time of capture: p = 0.4; Figure 2a). Body mass increased in March and April and peaked in early May (contrast: Mar-1 vs. May-1: $F_{1.1.499} = 350.9$, p < 0.0001) at a level 31.3% higher than that measured in March-1. Past this peak, M_b remained relatively stable from May to June (contrast: May-2 vs. Jun-3: p = 0.1) and gradually decreased from mid-June to July (by 23.4% contrast: Jun-2 vs. Jul-2: $F_{1,1505} = 231.3$, p < 0.0001). Body mass reached its nadir between mid-July and August (contrast: July-2 vs. Jul-3-Aug-2: p = 0.7). March values remained within a comparable range to those recorded at the peak of winter (contrast: Mar-1-Mar-3 vs. Dec-Feb: p = 0.08).

Temporal variation in fat mass was similar to that observed for $M_{\rm b}$ (month: $F_{26.692} = 104.4$, p < 0.0001; time of capture: $F_{1.745} = 4.7$, p < 0.05; Figure 2b), although we found no significant influence of structural body size (p = 0.3). From mid-March, birds increased their fat stores by 225.6% to reach 16.5 \pm 0.5 g of body fat in early May (contrast: Mar-1 vs. May-1: F_{1.886} = 288.3, p < 0.0001). Fat mass subsequently remained relatively stable until mid-June (contrast: May-2 vs. Jun-3: p = 0.14) and then decreased by 89.7% from mid-June to August (contrast: Jun-3 vs. Aug-1: $F_{1,856} = 248$, p < 0.0001) where it reached its lowest (1.2 \pm 0.5 g). From early April, fat mass surpassed winter values (contrast: Apr-1 vs. Dec-Feb: $F_{1,826} = 64.9$, p < 0.0001) and levels recorded in August were below those observed during the winter (contrast: Aug-1 vs. Dec-Feb: $F_{1,492}$ = 143.6, p < 0.0001). Regression analysis of monthly least square means revealed that most of the variation in $M_{\rm b}$ was driven by variation in body fat (n = 21, $r^2 = 0.96$, p < 0.0001; see insert Figure 2b).

Controlling for the effect of body size ($F_{1,89} = 26.2$, p < 0.0001), lean mass showed a different pattern to that of M_b and fat mass (month: $F_{26,1,223} = 76.0$, p < 0.0001, time of capture: p = 0.5; Figure 2c). Lean mass remained relatively stable, and comparable to winter values, at 24.1 \pm 0.1 g between mid-March and mid-June (contrast: Mar-1 vs. Jun-4: p = 0.3), with the lowest values recorded in May. Starting in June-4, lean mass then gradually increased (by



FIGURE 2 Intra-seasonal variation in body composition over 5 years in outdoor captive snow buntings. Data are least square means by period within months for body mass (a), fat mass (b) and lean mass (c). Least square means were obtained from mixed-effects models controlling for month with year and bird ID as random parameters. Least square means also control for structural body size in a and c (not significant for fat mass) and for time of capture in b (not significant for body mass and lean mass). Least square means per year (grey) were obtained from mixed-effects models controlling for the same parameters except year. Values on the left represent winter means extracted from those same models. Insert in Figure 2b shows the relationship between body mass and fat mass using monthly least square means generated by our mixed-effects models ($n = 21, r^2 = 0.96$. p < 0.0001). Data are least square means with error bars representing 95% confidence intervals

10.1%) to reach 27.3 \pm 0.4 g in August (contrast: Jun-4 vs. Aug-1: $F_{\rm 1.1,216} =$ 148.4, p < 0.0001).

Pectoral muscle thickness was related to structural body size ($F_{1.26} = 9.8$, p < 0.005) and varied significantly over time (month: $F_{16,346} = 24.2$, p < 0.0001, keel height: $F_{1,366} = 856.9$, p < 0.0001; Figure 3a). Between March-1 and April-2, size corrected values were stable (contrast: Mar-1 vs. Apr-2: p = 0.6) at 6.7 \pm 0.01 mm, and slightly lower than at the peak of winter (contrast: Mar-1-Apr-2 vs. Dec-Jan: $F_{1,350} = 35.4$, p < 0.0001), but still comparable to February (contrast: Mar-1-Apr-2 vs. Feb: p = 0.9). Then, muscle thickness gradually decreased by 7.8% between April-2 and July-2 (contrast: Apr-2 vs. Jul-2: $F_{1,348} = 94.1$, p < 0.0001) to reach its thinnest at 6.2 \pm 0.04 mm in July-2.

Finally, haematocrit also varied significantly over time (month: $F_{17,343} = 28.7, p < 0.0001$; Figure 3b). From March to early April it was high (contrast: Mar-1 vs. Apr-1: p = 0.9; 54.8 \pm 0.2%) and remained comparable to winter values until early May (contrast: Mar-1-May-1 vs. Dec-Feb: p = 0.5). Haematocrit gradually decreased between early April and August (contrast: Apr-1 vs. Aug-2: $F_{1,343} = 158.3, p < 0.0001$) to reach its lowest value (44.9 \pm 0.8%) by the end of August.

3.3 | Metabolic performance

Summit metabolic rate (M_{sum}), whether considered whole or corrected for lean mass ($F_{1.272} = 272.1$, p < 0.0001), varied over time

FIGURE 3 Intra-seasonal variation in pectoral muscle thickness and haematocrit in 2015 in outdoor captive snow buntings. Data are least square means by period within months for pectoral muscle thickness (a) and haematocrit (b). Least square means were obtained from mixedeffects models controlling for period with bird ID as a random parameter. Least square means in (a) also control for structural body size and keel length. Winter means extracted from those same models are also presented. Data are least square means with error bars representing 95% confidence intervals





(month for whole-animal M_{sum} : $F_{13,251} = 19.7$, p < 0.0001; Figure S1a; month for lean mass-independent M_{sum} : $F_{13,251} = 19.1$, p < 0.0001; Figure 4a). When considering the effect of lean mass, M_{sum} remained relatively stable between March and early May (contrast: Mar-1 vs. May-1: p = 0.5) and comparable to the coldest months of winter (contrast: Mar-1-May-1 vs. Dec-Feb: p = 0.3), at 3.40 \pm 0.03 W. Then, after remaining relatively high and near winter levels, it gradually declined before falling sharply in July and August (contrast: July-2 vs. Aug: $F_{1,251} = 33.6$, p < 0.0001). Regression analysis of monthly least square means revealed that variation in whole-animal M_{sum} was strongly positively associated with variation in size-independent pectoral muscle thickness (n = 10, $r^2 = 0.92$, p < 0.0001). This association remained strong for lean mass-independent M_{sum} ($n = 10, r^2 = 0.96$, p < 0.0001; Figure 5a). The latter was also strongly positively associated with variation in haematocrit (n = 11, $r^2 = 0.94$, p < 0.0001; Figure 5b).

Cold endurance, measured as the time needed to reach maximal heat production, showed a seasonal-related pattern similar to M_{sum} . Indeed, time to M_{sum} varied over the months ($F_{13,252} = 13.3$, p < 0.0001; Figure 4b; lean mass: p = 0.06). After surpassing winter values in March (contrast: Mar-1-Mar-2 vs. Dec-Feb: $F_{1,253} = 19$, p < 0.0001), values remained relatively stable (contrast: Apr-1 vs. May-2: p = 0.3) and comparable to those recorded at the peak of winter (contrast: Apr-1-May-2 vs. Dec-Feb: p = 0.4) before decreasing from the end of May to August (contrast: May-2 vs. Aug:

 $F_{1,252} =$ 46.8, p < 0.0001). At that point, birds were reaching their M_{sum} 3.2 times faster than in March (0.6 hr vs. 1.9 hr).

The temperature at which buntings attained their M_{sum} , whether considered raw or corrected for lean mass ($F_{1,244} = 4.8, p < 0.05$), also varied over time (month for whole-animal T_a at M_{sum} : $F_{13,229} = 7.6$, p < 0.0001; Figure S1b; month for lean mass-independent T_a at M_{sum} : $F_{13,231} = 8.0, p < 0.0001$; Figure 4b) and showed an opposite pattern to cold endurance (i.e. time to M_{sum}). In March, birds reached their M_{sum} at a T_a of -25.2 ± 1.8 °C in helox. Then, T_a at M_{sum} increased gradually and, by August, birds were attaining their M_{sum} at -9.3 ± 1.9 °C (contrast: Mar-2 vs. Aug: $F_{1,240} = 40.6, p < 0.0001$). Interestingly, the T_a at M_{sum} remained comparable to values recorded in winter throughout summer, with experimental temperatures in June and July still being similar to those obtained in December (contrast: Jun-1–Jul-2 vs. Dec: p = 0.4).

Basal metabolic rate (BMR), whether considered whole or corrected for lean mass ($F_{1,140} = 5.9$, p < 0.05) varied through the summer (month for whole BMR: $F_{13,258} = 4.9$, p < 0.0001; Figure S1c; month for lean mass-independent BMR: $F_{13,262} = 5.1$, p < 0.0001; Figure 4c). Controlling for the effect of lean mass, BMR increased by 13.4% between March-1 and April-2 (contrast: $F_{1,259} = 21.8$, p < 0.0001), remained relatively stable until June-2 (contrast Apr-2 vs. Jun-2: p = 0.9) at 0.54 \pm 0.004 W, a level surpassing that observed in winter (contrast: Apr-2–Jun-2 vs. Dec–Feb: $F_{1,258} = 22$, p < 0.0001) and then declined rapidly (by 16.3%) to reach its lowest level in July-2 (0.45 \pm 0.01 W; contrast Jun-2 vs. July-2: $F_{1,276} = 30.7$, p < 0.0001).



FIGURE 4 Intra-seasonal variation in metabolic performance in 2015 in outdoor captive snow buntings. Data are least square means by period within months for M_{sum} (a), time to M_{sum} and T_a at M_{sum} (b) as well as for BMR (c). Least square means were obtained from mixed-effects models controlling for period and lean body mass (not significant for time to M_{sum}) with bird ID as a random parameter. Winter means are extracted from those same models. Data are least square means with error bars representing 95% confidence intervals

3.4 | Moult intensity

Regression analysis, using monthly means extracted from mixed models, revealed a relatively strong positive relationship between lean body mass and moult intensity in buntings ($n = 7, r^2 = 0.68, p < 0.05$; Figure 6).

4 | DISCUSSION

This study was designed to determine whether and by which mechanism winter cold acclimatization can carry over to benefit subsequent migration and arrival/summer stages using cold specialized snow buntings as a model species. Specifically, we tested whether birds acclimated to cold winter conditions in early spring (a) experience additional phenotypic changes in preparation for migration, with consequent positive effects on thermogenic capacity (*migratory upregulation hypothesis*), or whether these birds are (b) already predisposed, in terms of thermogenic capacity and cold endurance, to migrate through cold northern environments, thus requiring no further changes in thermoregulatory traits (*thermal carryover hypothesis*). Typically, migratory species conform to the former hypothesis as they prepare for migration by increasing the size of several body components (e.g. fat stores, pectoral muscles, cardiopulmonary organs) and by elevating haematocrit and metabolic performance, which then confer additional benefits in terms of thermogenic capacity (Swanson, 1995; Zhang et al., 2015). However, changes in snow buntings did not fully match this pattern. Whereas body mass, fat mass and BMR increased relative to the winter phenotype as predicted by our *migratory upregulation hypothesis*, traits underlying cold endurance (i.e. lean mass, pectoral muscle thickness, haematocrit, M_{sum} and time to M_{sum}) remained stable, and high,



FIGURE 5 Relationships between M_{sum} and pectoral muscle thickness (a) and haematocrit (b) in outdoor captive snow buntings. Values are least square means generated by our mixed-effects models and are based on measurement periods between March and August in 2015. Error bars show 95% confidence intervals

into the months encompassing migration (March-May, Macdonald et al., 2012; McKinnon et al., 2016; Snell et al., 2018) and even into most of the summer, which is consistent with our *thermal carryover hypothesis*. In fact, both thermogenic capacity and cold endurance only showed the first clear signs of decline in July. Hence, for snow buntings our data suggest that phenotypic adjustments for winter cold acclimatization likely provide sufficient cold endurance for both their spring migration and arrival on the breeding grounds, and even possibly for breeding under unpredictable Arctic summer conditions.

4.1 | Changes in body composition only partially follow the typical pattern of migratory birds

4.1.1 | Increase in fat and total body mass for migration

As we predicted based on previous observations (Vincent & Bédard, 1976) and expectations under the *migratory upregulation*



FIGURE 6 Relationship between lean mass and moult intensity measured from June to October 2018. Values are least square means generated by mixed-effects models controlling for month and bird ID as random parameters. Least square means for lean mass also control for structural body size. Error bars represent 95% confidence intervals

hypothesis, snow buntings increased their fat mass by more than 200% in March and April and remained at elevated levels until the end of June. This pattern clearly drove variation in $M_{\rm b}$ (insert in Figure 2b), with a corresponding 31% increase. As with shivering, migratory flights are largely fuelled by lipids (Jenni & Jenni-Eiermann, 1998) and while buntings accumulate fat in winter (around 6 g, Le Pogam et al., 2020), winter fat levels are much lower than those observed during migration (17 g in May here). This seasonal difference in fat mass could therefore stem from the fact that, winter fat load reflects a balance between predation and starvation risks (Brodin, 2001, 2007) while in migration, birds are likely driven by the urgency to arrive early on their breeding grounds (Guindre-Parker et al., 2013). In fact, April fat stores represented an amount equivalent to 64% of buntings' lean (wet) body mass. This is comparable to values of 50%-70% reported in long-distance migrants crossing geographical barriers (Blem, 1980; Lindström & Piersma, 1993; Newton, 2008; reviewed by Guglielmo, 2018). Accordingly, buntings from our study population must cross the Labrador Sea to reach their Greenland breeding grounds (Macdonald et al., 2012).

While the increase in fat stores is consistent with the *migratory upregulation hypothesis*, buntings also maintained large fat stores late into the summer in direct contradiction with previous studies of captive migrants reporting declines in fat shortly after birds achieve a migratory phenotype (e.g. King et al., 1965; Piersma et al., 1995; Vézina et al., 2017). The reason(s) for the maintenance of fuel stores are not immediately clear, but a number of hypotheses can be formulated. Previous studies showed that fat storage can be governed by endogenous circannual processes independently from the immediate environment (Bairlein & Gwinner, 1994; Maggini & Bairlein, 2010; McWilliams et al., 2016; Piersma, 2002; Vézina et al., 2011). This timing mechanism could allow for maintaining stores beyond migration to cope with potentially harsh and unpredictable winter-type

conditions on Arctic-breeding grounds (e.g. Meltofte, 1983; Morrison et al., 2007; Walsh et al., 2005). However, temperatures on the winter range of buntings can be quite similar to those encountered during breeding (e.g. $-5.1 \pm 7.6^{\circ}$ C in May and June at Alert, NU, at the northern extreme of the species breeding range in Canada, compared to -9°C in our aviaries in January and February, Le Pogam et al., 2020) and wintering buntings do not maintain fat stores that large (Le Pogam et al., 2020). Maintaining fat stores later in summer could also serve as fuel for other energy-intensive activities such as establishing and defending territories in the spring, as well as breeding (Guindre-Parker et al., 2013; Macdonald et al., 2016). Maintenance of fat stores would allow males to spend less time foraging and more time on activities that promote reproductive success, such as display flights and aggressive pursuits, during a very short breeding season (Macdonald et al., 2012; Sandberg & Moore, 1996; Snell et al., 2018). More field data are required, however, to address these hypotheses.

4.1.2 | Maintenance of lean mass and pectoral muscle thickness at a winter level

As predicted by the *thermal carryover hypothesis*, buntings maintained constant, winter-level, lean mass and pectoral muscle thickness throughout their transition from wintering to migration phenotypes and into the summer. Snow buntings increase pectoral muscle thickness by 8% in winter (Le Pogam et al., 2020). This is associated with an improvement of shivering heat production (Liknes & Swanson, 2011; Petit et al., 2014; Swanson, 1991b), which is maintained for most of the summer (this study). Given that flight and shivering use the same muscle metabolic pathways (Marsh & Dawson, 1982; Wiersma et al., 2007), it is likely that the winter muscle phenotype provides the capacity required for this species to migrate through cold northern environments, as well as for breeding in unpredictable thermal conditions (Petit & Vézina, 2014; Walsh et al., 2005; Zhang et al., 2015).

As buntings were moulting their wing and tail feathers in July, we also observed a clear increase in lean body mass. The reasons underlying this change appear independent from requirements for thermoregulation (mean $T_a = 20.3 \pm 0.2$ °C in July and August) or migration (fall migration: September-November, Macdonald et al., 2012; McKinnon et al., 2016). Regression analysis, using monthly means extracted from mixed models, confirmed a relatively strong positive relationship between lean body mass and moult intensity (Figure 6), and suggests that postnuptial feather growth leads to an accumulation of new lean tissue. Synthesis and deposition of keratin increase considerably during moult (King & Murphy, 1990) and this is associated with the creation of new capillary networks to support keratin deposition (Kuenzel, 2003). The skin can also be fully regenerated during feather growth (up to 80.0 cm² of surface regenerated in white-crowned sparrow, Walsberg & King, 1978) and, interestingly, preliminary dissection data (A. Le Pogam et al. unpublished data) also show an increase in lean dry skin mass during moult in buntings. The spleen and thymus have also been shown to increase in mass during moult, possibly to cope with potential infections and parasites to which birds are more susceptible at that time (Anderson, 1970; Silverin et al., 1999). Some or a combination of these changes could contribute to the increase in lean mass observed here.

4.2 | Winter cold endurance carries over into migration and beyond

4.2.1 | Maintenance of thermogenic capacity and cold endurance at a winter level

Consistent with the thermal carryover hypothesis, we found that buntings maintained a high winter thermogenic capacity and cold endurance not only into the period of migratory fattening but also for a large part of summer, even at relatively warm temperatures. Our results therefore differ from those of previous studies that reported 10 to 25% increases in thermogenic capacity in association with the development of migratory phenotypes (Swanson, 1995; Vézina et al., 2007). It has been suggested that these performance increases are beneficial by-products from phenotypic adjustments for flight endurance rather than direct adjustments for thermogenesis (i.e. the migratory upregulation hypothesis, Swanson & Dean, 1999; Vézina et al., 2007; Zhang et al., 2015). Although this is likely, it appears that the opposite trend is at play in buntings. Seasonal increases in $M_{\rm sum}$ between summer and winter months are common in resident, non-migratory species (McKechnie et al., 2015) and we recently showed that these same captive buntings increase their M_{sum} by 27% during winter acclimatization (Le Pogam et al., 2020). Whether these birds could have increased M_{sum} further above their cold acclimatized phenotype is not clear and would require further study. However, the maintenance of winter thermogenic capacity through the migratory period does suggest that this level of metabolic output is sufficient to support migration in cold environments. It may also provide reserve capacity in cold endurance at later stages as birds can be surprised by harsh weather or snow storms during breeding (Meltofte, 1983). Overall, our results for thermogenic capacity and endurance as well as their associated traits lend strong support for the thermal carryover hypothesis. The winter phenotype confers a high level of cold endurance that is maintained during migration and even during the breeding period in snow buntings.

4.2.2 | Thermogenic capacity, pectoral muscle thickness and oxygen carrying capacity

Adjustments for flight endurance in preparation for migration are often characterized by increases in flight muscle mass (Dietz et al., 1999; Jehl, 1997; Marsh, 1984; Piersma et al., 1999), oxygen carrying capacity (Chilgren & DeGraw, 1977; Krause et al., 2016; Piersma, Everaarts, et al., 1996) and size of cardiopulmonary organs (Liknes & Swanson, 2011; Piersma et al., 1999; Zheng et al., 2008). In this study, pectoral muscles thickness and haematocrit were maintained at winter levels throughout the migratory period and for a good part of summer. Given their likely role in promoting thermogenic capacity in this species (Dubois et al., 2016; Le Pogam et al., 2020) these parameters surely contributed to maintain the high, winter-level, M_{sum} observed during that time, as shown by the positive relationships in Figure 5. Interestingly, both whole and lean mass corrected M_{sum} were correlated with pectoral muscle thickness. As statistically controlling for lean mass should largely remove the effect of skeletal muscle mass on M_{sum} (e.g. skeletal muscles contribute to 73% of lean M_b in black-capped chickadee, Poecile atricapillus, M. Petit & F. Vézina unpubl. data), this observation is consistent with an influence of muscle metabolic processes at the cell level in regulating thermogenic capacity (Milbergue et al., 2018; Noakes et al., 2020; Stager et al., 2015; Vézina et al., 2011). These results, therefore, further support the thermal carryover hypothesis as adiustments previously made for cold acclimatization are maintained throughout migration.

4.2.3 | Migration-related changes in basal metabolic rate

Basal metabolic rate increased by 13% and followed a pattern similar to that of body and fat mass throughout the migration and summer periods. In contrast with thermogenic capacity and cold endurance, this pattern is thus consistent with the migratory upregulation hypothesis and is similar to that observed in other migratory species (Piersma et al., 1995; Swanson & Dean, 1999). However, lean mass, a known contributor to physiological maintenance costs (Piersma, Bruinzeel, et al., 1996; Piersma et al., 2004; Swanson, King, et al., 2017) remained relatively constant during that time and variation in BMR was still observed when statistically considering its effect. This therefore suggests that BMR variation at this stage originates from tissue level activity supporting the migratory phenotype rather than from a change in mass of metabolically active tissues (Guglielmo et al., 2002; McKechnie, 2008; Piersma et al., 2004; Vézina et al., 2017; Vézina & Williams, 2005). Note that high levels of summer BMR have also been reported in other Arctic-breeding species (Jetz et al., 2008; Kvist & Lindström, 2001).

5 | CONCLUSIONS

This study investigated phenotypic adjustments during the transition from winter to migration and summer in a cold specialized songbird and evaluated how specific phenotypic traits associated with cold endurance and flight performance conformed to two newly formulated hypotheses, the *migratory upregulation* and *thermal carryover hypotheses*. We have shown that specific traits such as body mass and BMR change to support migration, while other traits such as thermogenic capacity and cold endurance remain constant at winter levels throughout the migratory transition and beyond. Therefore, this study not only demonstrates that basal and maximal traits of metabolic performance can vary independently as previously observed (Barceló et al., 2017; Dubois et al., 2016; Petit et al., 2013) but also that winter cold acclimatization in this cold specialist likely provides sufficient aerobic performance for migration in relatively harsh cold environments (Zhang et al., 2015). Maintaining high thermogenic capacity through migration and beyond likely contributes to the ability of males to migrate very early in thermally inhospitable conditions to secure the best breeding territories well ahead of the commencement of breeding (Macdonald et al., 2012; Snell et al., 2018). While our findings may appear exceptional, it should be noted here that several other passerines species also winter in cold temperate areas and breed in Arctic regions (e.g. common redpoll Acanthis flammea, lapland longspur Calcarius lapponicus, white-crowed sparrow, horned lark Eremophila alpestris). We therefore expect the findings reported here to be typical of these long-distance migrant cold specialists rather than specific to snow buntings, although this idea will require more research. Our collective results are the first direct demonstration that specific phenotypic traits underlying cold endurance can positively carry over into a migratory phenotype independently from traits, such as fat storage, requiring considerable body transformation and maintenance costs. Presumably, this thermogenic capacity in buntings provides a competitive advantage to colonize Arcticbreeding habitats up to the northern edge of terrestrial land.

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AUTHORS' CONTRIBUTIONS

A.L.P. and F.V. conceived the ideas and designed methodology; A.L.P., M.P. and L.R. collected the data; A.L.P. analysed the data; A.L.P., R.S.O., 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 STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/ dryad.7d7wm37tt (Le Pogam et al., 2021).

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