JOURNAL OF
AVIAN BIOLOGY

Article

Flexible response to short-term weather in a cold-adapted songbird

Marie-Pier Laplante, Emily A. McKinnon, Oliver P. Love and François Vézina

M.-P. Laplante (Marie-Pier.Laplante@uqar.ca) (http://orcid.org/0000-0001-9034-8585) and F. Vézina (http://orcid.org/0000-0002-4990-5391), Univ. du Québec à Rimouski, Dépt de biologie, chimie et géographie, Groupe de recherche sur les environnements nordiques BORÉAS, Centre d'Études Nordiques, Centre de la Science de la Biodiversité du Québec, Rimouski, QC, Canada. – E. A. McKinnon (http://orcid.org/0000-0003-3631-0644) and O. P. Love (http://orcid.org/0000-0001-8235-6411), Univ. of Windsor, Dept of Biological Sciences, Windsor, ON, Canada. Current address of EAM: Access and Aboriginal Focus Programs, Extended Education, Univ. of Manitoba, Migizii Agamik, Winnipeg, MB, Canada.

Journal of Avian Biology
2019: e01766
doi: 10.1111/jav.01766

Subject Editor: Suvi Ruuskanen
Editor-in-Chief: Jan-Åke Nilsson
Accepted 3 December 2018

To improve survival during winter, temperate species use a variety of behavioural and physiological adaptations. Among songbirds, the maintenance of lipid reserves is a widely-used strategy to cope with the severity of winter; however, little is known regarding how multiple synchronously acting environmental mechanisms work together to drive these effects. In a context where temperate winter conditions are becoming more variable, it is important to widen our understanding regarding the flexible adaptations that may allow wintering species to adjust to projected climate change. Using a long-term dataset collected across multiple wintering populations (7 years; 8 locations), we analyzed the effects of daily variation in weather (e.g. temperature, snowfall) on the variation in energy reserves (i.e. fat stores) of wintering snow buntings *Plectrophenax nivalis*. Our results support the prediction that birds carry more reserves to increase the safety margin against starvation when conditions are energy-demanding and access to food is unpredictable (i.e. colder, snowier conditions). Birds responded to daily changes in weather by increasing their reserves as conditions deteriorated, with maximal temperatures and snow depth being the most important predictors of fattening decisions. We also found that females consistently exhibited higher fat reserves than males relative to their body size, suggesting that differential physiological adaptations among sexes or social dominance may play an additional role in explaining variation in energy reserves across individuals in this species. Overall, our findings increase knowledge on phenotypic adjustments used by species wintering in temperate zones to match variation in their environment.

Keywords: avian energetics, snow bunting, winter acclimatization

Introduction

For small endotherms inhabiting temperate regions, winter can be a particularly challenging period (Cooper 2000). Not only does shortened day length reduce the time available for foraging, but cold temperatures increase energy expenditure for thermoregulation (Scholander et al. 1950) and adverse weather conditions such as

NORDIC SOCIETY OIKOS
www.avianbiology.org

storms can reduce access to food resources (King 1972, Carey 2012). Overwintering species have evolved a range of anatomical, behavioural and physiological adaptations selected to improve survival during harsh or unpredictable conditions (Heinrich 2009). Among small songbirds, an increase in lipid reserves during winter is a widely-used strategy to cope with the severity of climatic conditions (Dawson and Marsh 1986, Haftorn 1989, see Blem 1990 for a review). Fat reserves are accumulated during the day, acting as the principal source of energy to survive fasting through the night, while also offering a safety margin against starvation in case finding food becomes difficult during the subsequent day(s) (Blem 1976, Lehikoinen 1987).

Despite its energetic benefits, accumulating and carrying fat reserves does entail significant costs (reviews by Witter and Cuthill 1993, Cuthill and Houston 1997). For example, individuals increase exposure to predation while looking for resources as they spend more time feeding to enlarge or maintain their lipid reserves (McNamara and Houston 1990, Brodin 2007). Carrying a heavier body during flight also entails elevated energy costs (Brodin 2001) while ultimately this extra mass can increase predation risk by impairing flight and take-off abilities (Hedenström 1992, Metcalfe and Ure 1995, Lilliendahl 1997, Dietz et al. 2007). Accordingly, both theoretical (Lima 1986, Macleod et al. 2005, Krams et al. 2010, Bonter et al. 2013) and empirical observations Houston and McNamara 1993, (Houston et al. 1993, Bednekoff and Houston 1994) have confirmed that birds optimize the storage of lipids to avoid starvation while minimizing mass gain to reduce predation risks.

To adjust their energy reserves to ambient conditions, birds may therefore flexibly fine-tune the size of their fat reserves in direct response to local daily changes in weather (i.e., a proximate response to variable weather conditions, see Pravosudov and Grubb 1997 for a review). For instance, species such as the white-throated sparrow (*Zonotrichia albicollis*; Blem and Shelor 1986) and dark-eyed junco (*Junco hyemalis*; Nolan and Ketterson 1983) have more body fat on days where the need for insurance against starvation is greater (i.e. cold weather) (King 1972, Ekman and Hake 1990, Bednekoff and Krebs 1995, but see Gosler 2002). Ambient temperature (Balen 1967, Newton 1969, Polo et al. 2007, Goławski et al. 2015) and, to a lesser extent, wind speed (Kelly et al. 2002, Goławski et al. 2015), humidity (Blem and Shelor 1986) and snow cover (Nolan and Ketterson 1983, Broggi et al. 2003) have all been shown to influence short-term adjustment of energy reserves in birds. However, to date, few studies have looked at the relative importance of these variables in driving daily fattening (although see: Vincent et Bédard 1976, Blem and Shelor 1986). Furthermore, most studies on winter fattening have been conducted in relatively mild winter environments, with little snow accumulation and/or where marine currents moderate temperature extremes despite high latitude (Newton 1969, Lehikoinen 1987, Haftorn 1989, Gosler 1996). Understanding the relative influence of environmental variables on energy budgets and reserve management is especially relevant as species face increasing uncertainties in both short-term weather patterns and larger-scale climatic variation as a result of climate change (Deser et al. 2012, Williams et al. 2015).

In this study, we investigated flexible adjustments of winter energy reserves across multiple wintering populations of snow buntings *Plectrophenax nivalis*, a circumpolar Arctic-breeding migratory songbird wintering in snow-covered habitats. Specifically, we examined energy reserve dynamics in response to daily variation in multiple weather variables. This species offers an ideal system to examine the relative influence of weather parameters on winter energy reserves as it winters in regions where low temperatures, frequent snow fall (limiting access to food) and highly variable weather conditions should promote selection for short-term flexibility in energy management (Cavieres and Sabat 2008). Snow buntings also form flocks of up to 1000 individuals during the winter (Montgomerie and Lyon 2011) and are readily captured in large numbers (up to 200 individuals in a day). The recent instigation of a citizen science project focused on the species across eastern Canada provided a unique opportunity to obtain a large dataset to study daily fattening over a large geographic range.

We proceeded on the long-held assumption that the amount of fat stored by an individual reflects the perceived demand for safeguard against starvation while minimizing predation risks (Lima 1986, Lehikoinen 1987, Bednekoff and Houston 1994). We aimed to test whether birds show short-term flexibility in the management of their energy reserves, and to quantify the relative importance of weather variables in predicting daily fattening decisions. We predicted that if birds fine-tune energy reserves to variation in local weather, they should carry more fat on days where the probability of starving is higher, that is the days with increased snow depth or snow fall limiting access to food and increased wind gusts or low temperatures leading to higher heat losses. Considering that age and sex classes may reflect differential dominance status and/or previous site-experience, we expected that it may have an influence on energy budgets amongst individuals (Gosler 2002). Alternatively, given that males are usually larger and heavier than females, birds of different sex or age classes may also differ in their physiological responses to local conditions (Smith 1994).

Material and methods

Field methods and capture data

For this study, bird banding (ringing) data was obtained from the Canadian bird banding office (BBO) for the period 2009–2015. Additional data on body mass, wing chord, fat score and time of capture were obtained from the citizen science project Canadian snow bunting network (CSBN). We kept only individual records for which a complete set of information was available for every individual (i.e. sex, age,

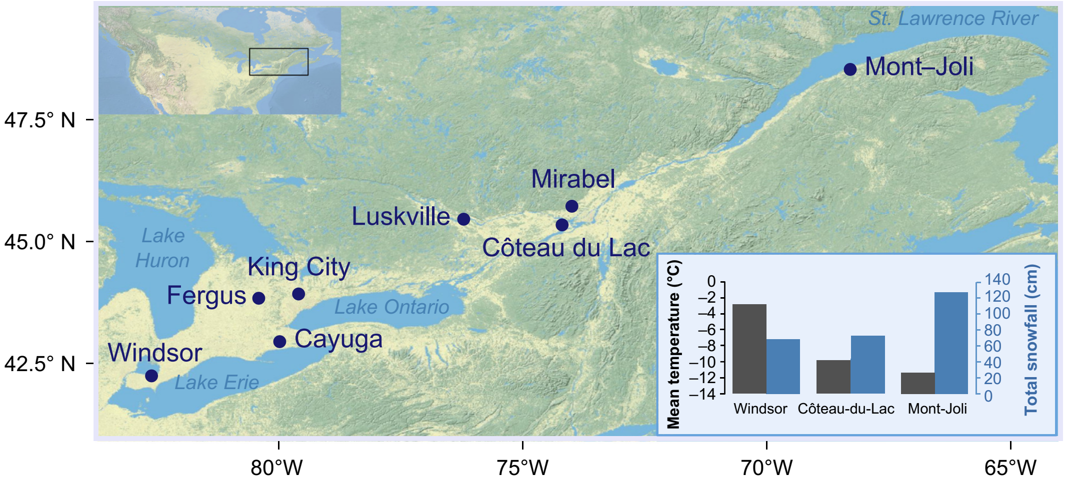

Figure 1. Geospatial extent of study area with bird banding locations included in the analyses. Thirty-year climate normals for the period 1981–2010 (for total snowfall and temperatures) at three of the locations are shown, highlighting the presence of a gradient of climate harshness across locations of the study area.

wing chord, fat score, body mass, time of capture), representing a total of 12 245 individual birds captured in eastern Canada (Fig. 1). Each winter, snow buntings were captured across wintering locations forming a climatic / weather gradient represented by a spread across both latitude and longitude (Fig. 1). There are marked differences in long-term mean temperatures and total snowfall across these locations (Fig. 1), two parameters that are known to strongly affect the regulation of body reserves in small wintering passerines (Waite 1992). At each site, birds were captured in open agricultural or coastal areas using seed-baited walk-in traps. Sex and age were determined morphologically according to Pyle (1997) and birds were banded with a unique numbered aluminum band (United States fish and wildlife service). Unflattened wing chord was measured to the nearest 1 mm, as an index of structural body size, and body mass was recorded to 0.1 g using an electronic scale. The size of fat reserves was also estimated visually using a standardized scoring system ranging from 0–7 (0 = no fat, furculum region is concave; 7 = pads of furculum and abdomen meet, Canadian snow bunting network protocol).

Weather data

Daily weather variables were extracted from the following three sources: 1) environment and climate change Canada (ECCC) weather office online (<www.weatheroffice.gc.ca>), 2) ministère du développement durable de l'environnement et de la lutte contre les changements climatiques (MDDELCC), and 3) national snow and ice data center (NSIDC) (Brown and Brasnett 2010). For daily data obtained from ECCC and MDDELCC, banding site coordinates were used to determine the weather station closest to each banding site (mean distance: 13.69 ± 7.24 km, mean ± SE, range = 4.47–25.28 km). We also used these coordinates to extract snow depth data from the NSIDC (see Brasnett (1999) and Brown and Brasnett (2010) for details on daily snow depth analysis calculations), using only the grid cells (24 × 24 km) that included banding locations. In total, we extracted eight daily weather variables predicted to be biologically relevant for snow bunting wintering energetics: mean temperature (°C), minimal temperature (°C), maximal temperature (°C), snow depth (cm), total snowfall (cm), absolute humidity (g m^{-3}), maximal wind gust (km h^{-1}), cloud cover (0–10) (variables and units are summarized in Supplementary material Appendix 1 Table A1). In addition to mean values for the day of capture, we also examined mean weather variables for the three-day window prior to the capture date of every bird since it is generally assumed that birds may use the recent past weather to determine the level of reserves to be accumulated the next day (Bednekoff et al. 1994).

Statistical analyses

Estimation of energy reserves

Interpretations with regards to stored energy in birds may potentially vary depending upon the metric that is being used to assess fat reserves: we therefore used two indexes of fat reserves in our statistical analyses. We first considered body mass because winter variation in mass is strongly influenced by the amount of fat carried by birds (Dawson and Marsh 1986, Rogers 1987). However, several studies have also shown significant increases in non-fat body components, such as flight muscles (Swanson and Vézina 2015) or digestive organs in association with cold wintering conditions in passerines (Zheng et al. 2008, Liknes and Swanson 2011, Petit et al. 2014). Therefore, interpreting body mass variation alone as an indicator of fat reserves could be partly biased as it is also influenced by lean components of body mass. Thus, we also used visual fat score to assess the extent of fat reserves more directly. Although fat scores can be affected by observer bias (Rogers 1991), this measure has nevertheless been shown to be a good predictor of true fat content in other passerine species (see examples in Krementz and Pendleton 1990). It is also commonly available within banding databases (Krementz and Pendleton 1990, Dunn 2003) as it is an easy and inexpensive technique to assess fat stores in wild-caught birds. Furthermore, our current work on captive snow buntings using quantitative magnetic resonance to precisely and non-invasively estimate body fat mass (Guglielmo et al. 2011) indicates that 75% of the variation in body fat is explained by fat score, confirming that fat scores reliably predicts body fat content in this species, despite possible observer bias (Le Pogam, Love and Vézina in prep.). Nonetheless, to increase overall confidence in our model outputs, we first ran analyses using body mass alone as our index of energy reserves, followed by the same analyses using fat score alone as a response variable to confirm that the observed trends were likely driven by variation in fat content.

The effect of structural size on body mass and fat reserves is well known in passerines given that structurally larger birds are usually heavier and can hold larger amounts of fat (Balen 1967, Blem 1990). The effects of time of capture on body mass and fat reserves are also well documented, as birds are fattening throughout the day during winter (Karpouzos et al. 2005, Turcotte and Desrochers 2008, Mandin and Vézina 2012). Photoperiod also influences variation in daily fat reserves, as birds store more fat when days are shorter because they have to sustain longer nocturnal fasts (Lehikoinen 1987, Mandin and Vézina 2012). Therefore, we corrected our indexes of fat reserves for these potential confounds by first extracting residual body mass/fat from models testing for relationship with these independent variables (structural size, time of capture and day length) after confirming their effects (see results section). These residuals were then used as our new (i.e. corrected) dependent variables for all subsequent analyses. Note that we opted for the extraction of residuals instead of including the confounding variables as predictors in the models, because it allowed for simplifying models, which already contained a large number of predictors. The use of this method was further motivated by the fact that day length and time of capture, when included as covariates in models including weather variables, generated severe multicollinearity issues as confirmed via variance inflation factor (VIF) analyses (e.g. VIF = 84–85; adapted from Fox and Weisberg 2010). Body mass residuals were also regressed against fat score to confirm that this variable indeed reflected variation in fat reserves (Supplementary material Appendix 1 Fig. A1). Thereafter, residual mass and residual fat score are simply referred to as 'body mass^{R}' and 'fat score^{R}'.

We worked with data collected between 1 Nov and 20 Mar to include only the wintering period for snow bunting populations within eastern North America (Vincent and Bédard 1976, Montgomerie and Lyon 2011, McKinnon et al. 2016). We tested for the effect of weather (both for the day of capture and the three-day average prior to capture) on both 1) fat score^{R} and 2) body mass^{R} using linear mixed-effect models (Raudenbush and Bryk 2001). Because predictor variables were on different scales, all numerical variables were standardized using the scaling method implemented in R package 'arm' (Gelman and Su 2008). This method allows the resulting coefficients to be directly comparable with binary predictors in our models, such as sex and age (Gelman 2008). Capture site and year were included as random effects. Wind speed and cloud cover could not be included in the three-day prior models because of missing weather data. To reduce multicollinearity, predictor variables having VIF values above 10 (Menard 1995, Neter et al. 1989, Hair 1998) were sequentially eliminated from the full model until all were below 10 (only the variable mean temperature was removed). Subsequently, we calculated the average VIF across predictors to ensure that the value was not substantially greater than 1 (Chatterjee and Price 1991).

The description of predictors used in the full model can be found in Supplementary material Appendix 1 Table A1. Once the predictors to be included in the full models were defined, we derived all possible submodels from each set of predictors (Stokke et al. 2008, Grueber et al. 2011). An Akaike information criterion value (AIC) was then calculated for all models. Based on selection by the AIC, the model with the lowest Δ AIC among those falling within Δ AIC < 2 was retained for interpretation. We also used a likelihood ratio test of the best model compared to a null model to determine if weather was a significant factor in explaining variation of energy reserves. Variables were considered significant when their confidence intervals did not include zero. Only banding entries with an associated complete set of weather variables were kept in this dataset to avoid conflicts with model selection (final sample size = 11 119 birds).

All statistical analyses were conducted using the statistical software R 3.2.1 (R Core Team). The function 'lmer' (linear models) in the package lme4 was used to run mixed-effects models (Bates et al. 2015). The function 'dredge' in the package MuMIn was used for model selection (Barton 2009). The function 'sem.model.fit' was used to extract R^2 for mixed models in the package 'piecewiseSEM' (Lefcheck 2016) and the function 'rsq.partial' was used to extract partial R^2 for multiple regression models in the package 'rsq' (Zhang 2017). All values are reported as mean ± SEM.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.f7h4614> (Laplante et al. 2019).

Results

Estimation of energy reserves

Body mass was positively correlated with fat score ($R^2 = 0.187$, $F_{2.67,12\,243} = 2813$, $p < 0.001$). Structural size was a significant predictor of both body mass ($\beta = 0.466 \pm 0.006$, $p < 0.001$) and fat score ($\beta = 0.065, \pm 0.003$, $p < 0.001$). Although very weak, the latter effect was surprising as visual fat scores are ranked relative to the size of the bird (e.g. furcular area), meaning that the metric should already be correcting for body size. However, as this could potentially reflect some observer bias (e.g. a tendency to score structurally large birds higher), we adopted a conservative approach and included structural size in the fat score model when calculating residuals. There was also a significant positive effect of time of capture (time of day at which the bird is captured) on both body mass ($\beta = 3.477 \pm 0.266$, $p < 0.001$) and fat score ($\beta = 0.973 \pm 0.148$, $p < 0.001$). Furthermore, day length negatively predicted body mass ($\beta = -0.356 \pm 0.023$, $p < 0.001$) and fat score ($\beta = -0.198 \pm 0.013$, $p < 0.001$). Therefore, birds were heavier and had higher fat scores when they were structurally larger, were captured later in the day and when days were shorter. Controlling for these effects, residual body mass was still significantly correlated with fat score ($n = 12\ 245$, $R^2 = 0.145$, $F_{1,12243} = 2070$, $p < 0.001$, Supplementary material Appendix 1 Fig. A1).

Influence of weather parameters on energy reserves

Models using weather associated with the focal day of capture explained slightly more variance and had lower AIC values than models using weather averaged over the three days preceding capture (Table 1, see Fig. 2 for the weather variables retained in each of the four best models; see Supplementary material Appendix 1 Table A2 for the list of models falling within Δ AIC 2 for each of the 4 full models on which selection was performed). Weather variables also explained the variation in fat reserves better than the variation in body mass (e.g. fat score: 36%; body mass: 15%) (see conditional R^2, Table 1). All models were significantly stronger than the associated null models (fat score: $\chi^2_9 = 572$, $p < 0.001$; three-day-prior fat score: $\chi^2_8 = 454$, $p < 0.001$; body mass: $\chi^2_8 = 262$, $p < 0.001$; three-day-prior body mass: $\chi^2_6 = 176$, $p < 0.001$) and had lower AIC values (Table 1).

Seasonal changes in energy reserves

When considering the focal day of capture we found that birds were heavier and had larger fat reserves as the season progressed (ordinal day effect on body mass^R: $z = 3.025$, $\beta = 0.163 \pm 0.054$; ordinal day effect on fat score^R: $z = 6.138$, $\beta = 0.158 \pm 0.026$; Fig. 2A, C). The same effect was found for fat score when considering the three days preceeding capture ($z = 3.998$, $\beta = 0.112 \pm 0.028$), although ordinal day was not retained in the three-day-prior models explaining residual body mass variation (Fig. 2B, D).

Snow depth and snow fall

On the day of capture, both body mass^R and fat score^R increased with increasing snow depth (body mass^R: $z = 4.148$, $\beta = 0.285 \pm 0.069$; fat score^R: $z = 7.095$, $\beta = 0.235 \pm 0.033$, Fig. 2A, C). The same pattern held true for models considering 3-day average weather (effect of snow depth on body mass^R: $z = 6.797$, $\beta = 0.404 \pm 0.060$; effect of snow depth on fat score^R: $z = 6.635$, $\beta = 0.227 \pm 0.034$, Fig. 2B, D). However, while snowfall on the day of capture was a positive and significant predictor of fat score^R ($z = 3.573$, $\beta = 0.075 \pm 0.021$, Fig. 2C), this variable was not retained in the model explaining variation in body mass^R (Fig. 2A). Again, the same pattern was found for models using 3-day average weather (effect of three-day prior snowfall on fat score^R only: $z = 3.210$, $\beta = 0.068 \pm 0.021$, Fig. 2A, D).

Ambient temperature

Body mass and fat reserves showed complex relationships with temperature variables, where both body mass^R and fat score^R increased as maximal temperatures declined (body mass^R: $z = -9.322$, $\beta = -5.117 \pm 0.055$; fat score^R: $z = -11.962$, $\beta = -0.310 \pm 0.026$), yet both decreased with declining minimal temperatures (body mass^R: $z = 3.830$, $\beta = 0.237 \pm 0.062$; fat score^R: $z = 4.912$, $\beta = 0.145 \pm 0.029$, Fig. 2A, C). This pattern was also observed when considering 3-day averages. Body mass^R and fat score^R increased as three-day prior maximal temperatures declined (body mass^R: $z = -1.922$, $\beta = -0.160 \pm 0.083$; fat score^R: $z = -5.348$, $\beta = -0.225 \pm 0.042$) and both decreased with declining three-day prior minimal temperatures (body mass^R: $z = 3.746$, $\beta = 0.359 \pm 0.096$; fat score^R: $z = 4.767$, $\beta = 0.222 \pm 0.047$) (see Fig. 2B, D).

Humidity

Variation in absolute humidity predicted variation in daily fattening, but only when weather variables were averaged over the previous three days (Fig. 2B, D). Indeed, birds had a lower body mass^R ($z = -2.685$, $\beta = -0.317 \pm 0.118$) and fat score^R ($z = -2.452$, $\beta = -0.138 \pm 0.056$) when the three days preceding capture had been more humid. Humidity on the

Table 1. Statistics for the four retained models for analyses on daily variation of energy reserves in snow buntings ($n = 11\ 119$ for each model). 'Rfat' and 'Rmass' refer to models using weather associated with the focal day of capture, with residual mass and fat score as a response. 'Rfat3' and 'Rmass3' refer to models using weather averaged over the three-day preceding capture, with residual mass and fat score as a response. Marginal R^2 is based on the fixed effects alone and conditional R^2 incorporate the random effects.

Models	R^2 Marginal	R^2 Conditional	AIC	AIC null	Random effect variance station | year	Residual
Rfat	0.037	0.363	32456	33010	0.458 | 0.094	1.0773
Rfat3	0.030	0.351	32572	33010	0.442 | 0.097	1.0891
Rmass	0.027	0.153	49171	49417	0.661 | 0.064	4.8509
Rmass3	0.023	0.149	49254	49417	0.651 | 0.065	4.8904

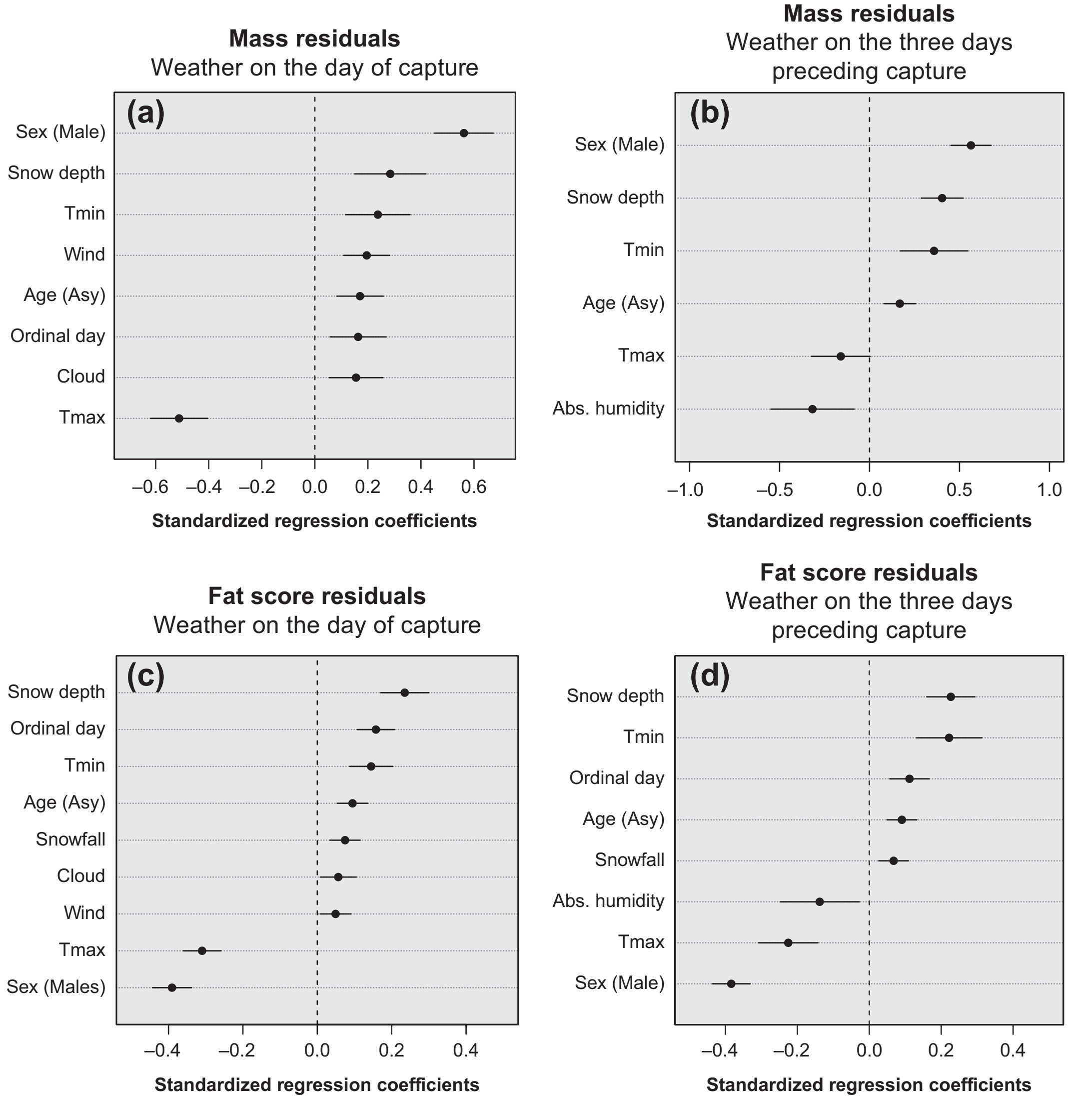

Figure 2. Standardized regression coefficients of parameters retained in the selected models. Upper panels are results for the best model of residual residual body mass as a function of variables on the day of capture (a) and as a function of mean average of variables on the 3 days preceding capture (b). Bottom panels show results for the best model of residual fat score as a function of variables on the day of capture (c) and as a function of mean average of variables on the 3 days preceding capture (d). Bars represent the 95 % confidence interval of the coefficients. Variables whose error bars include 0 are considered not significant.

day of capture was not a predictor of either a bird's body mass^R or its fat score^R.

Cloud cover and wind speed

Cloud cover and wind speed also predicted variation in body mass^R and fat score^R of birds captured on a given day: individuals tended to be heavier and fatter when days were cloudier (body mass^R: $z=3.004$, $\beta=0.155 \pm 0.051$; fat score^R: $z=2.274$, $\beta=0.056 \pm 0.024$) and windier (body mass^R: $z=4.420$, $\beta=0.196 \pm 0.055$; fat score^R: $z=2.328$, $\beta=0.045 \pm 0.021$). However, these effects were weak considering the low β values and confidence intervals almost including zero (Fig. 2A, C). These variables could not be studied in 3-day-prior models due to missing data (see Methods).

Age and sex

All models revealed that after second year (ASY) birds were significantly heavier and fatter than birds in their second year of life (SY) (body mass^R: $z=3.810$, $\beta=0.170 \pm 0.045$; fat score^R: $z=4.498$, $\beta=0.095 \pm 0.021$, Fig. 2A–D). Sex was also an important predictor of both body mass and fat score in all models. Indeed, males were heavier than females (body mass^R: $z=9.916$, $\beta=0.562 \pm 0.057$, Fig. 2A, B) while carrying less fat (fat score^R: $z=-14.592$, $\beta=-0.391 \pm 0.027$, Fig. 2C, D). The same tendencies were observed when using weather averaged over the three days preceding capture (see also inter-sexual differences in energy reserves for each station separately in Supplementary material Appendix 1 Table A3–A4, Fig. A2–A3).

Discussion

Few studies have attempted to provide a thorough examination of how multiple weather parameters influence energy reserve management in wintering birds. Using a large multi-site dataset we found support for the prediction that snow buntings respond to both short- and longer- (3 day) term changes in several weather variables acting in parallel, such as snow cover, wind and temperature. Our data are consistent with birds carrying more fat when there is a greater probability of starvation (Carey and Dawson 1999). Interestingly, inter-sexual variation in body mass and fat reserves suggests that constraints of wintering likely differ between sexes in this species.

Fine-tuning of energy reserves to meet daily weather challenges

As predicted, snow buntings appear to fine-tune their energy reserves in response to short-term changes in weather. Such phenotypic flexibility is expected to evolve in species facing variable environmental conditions such as fluctuating food resources and changing weather (Caswell 1983, Cavieres and Sabat 2008). Individual birds increased the size of their energy reserves as weather conditions increased in severity, (e.g. as snow depth increased both body mass and fat score increased), a finding consistent with previous work on snow buntings held in captive outdoor conditions (Vincent and Bédard 1976). These results were expected given that snow cover limits access to food for wintering granivorous ground-foraging birds such as snow buntings and has been found to decrease the abundance of these species in winter (Best et al. 1998). Short-term adjustment of energy reserves in response to snowfall has also been observed in other small wintering passerines (Nolan and Ketterson 1983, Blem and Shelor 1986, Ekman and Hake 1990, Waite 1992, Broggi et al. 2003, Rogers and Reed 2003).

Snow buntings also maintained greater energy reserves when maximal temperatures decreased, supporting our prediction that birds should be heavier and fatter when heat loss increases energy demands. However, the direction of the relationship was opposite for minimal temperatures, whereby birds were lighter and had lower fat scores when minimal temperatures declined. While a negative relationship with maximal temperature may indicate strategic fattening, a positive relationship with minimal temperatures suggests that snow buntings may be constrained in their capacity to fatten on very cold days. In fact, birds might be forced to use a greater proportion of their energy input during the day and/or be forced to use their reserves at a higher rate during these days (see Mandin and Vézina 2012 for a similar case in black capped chickadees *Poecile atricapillus*). Our results therefore suggest that maximal and minimal temperatures can influence avian energy budgets differently in a context-depent manner. We therefore recommend caution when analyzing the influence of temperature in energtic studies, especially when using only daily average values. We suggest considering both maximal and minimal temperatures in studies on fattening.

The observation of a negative relationship between fat reserves and absolute humidity measured during the 3 days preceding capture is interesting. Mandin and Vézina (2012) reported that black-capped chickadees consumed more of their fat reserves during humid periods (based on relative humidity) measured up to 7 days before capture, which is consistent with our results. Likewise, Petit et al. (2013) also reported an effect of absolute humidity on summit metabolic rate in that same species, with birds expressing higher cold endurance during humid days. As humid air may increase heat loss through evaporative cooling of water condensing on the body, periods of higher humidity could lead to higher daily energy expenditure and lower fat reserves. However, this should mostly be limited to periods where ambient temperatures are above freezing (Petit et al 2013). Although we do not have data on their occurrence, such humid periods could also be associated with icing, thus reducing access to food and forcing the use of fat reserves. Still, we suggest interpreting this result with caution since confidence intervals were very large for both body mass and fat scores, indicating significant variability in the response, which almost included zero for the analyses on fat score^{R}.

We found that variation in weather conditions explained daily variation in fat score much better than variation in total body mass (Table 1). Fat score also seemed to be more fine-tuned to weather parameters than body mass. For example, our data indicate that fat score was related to snowfall (in addition to snow depth), which could be perceived as an important cue that food is becoming less available, while body mass was only related to snow depth. Interestingly, this suggests that a visual approximation of fat reserve size such as a visible fat score may be more appropriate when using large datasets in quantifying fat reserves than size-corrected body mass in small wintering passerines. Studies have shown that the non-fat component of avian body mass (i.e. organs, muscles) varies seasonally, culminating at the peak of winter, rather than on a short term basis like fat reserves (Liu and Li 2005, Zheng et al. 2008, Petit et al. 2014). This could explain why body mass was less influenced by weather than fat score in this study.

The importance of sex and age in winter energy levels

We found that females carried more energy reserves than males for a given body size and that, although the effect was weaker, older birds carried more energy reserves than younger birds (Fig. 2, see also Supplementary material Appendix 1 Fig. A2–A3). This provides support to a similar, but non-significant, trend reported in snow buntings by Macdonald et al. (2015), suggesting that sex is more important than age in influencing energy management in this species. This difference in energy levels across sex and age classes could potentially be related to social status (Ficken et al. 1990, Ekman and Lilliendahl 1993) as in passerines dominant individuals are typically leaner than subordinates because their status provides priority over resources (Clark and Ekman 1995). In snow buntings, males are indeed dominant over females, and younger birds (contrary to many other species) are dominant over older birds (Smith and Metcalfe 1994). However, teasing apart the influence of sex-related dominance and weather on snow buntings' energy management will require further experimental work as ongoing studies in our laboratory show the same sex differences in wintering outdoor captive birds kept in single-sex pens, where social interactions among males and females are not possible.

For a given structural body size, while males carried less fat than females, they were nonetheless heavier (Fig. 2, see also Supplementary material Appendix 1 Fig. A3). This suggests that male and female snow buntings may not apportion body components the same way. For example, for their size, the higher mass of wintering males may not be driven by a larger amount of fat, but instead could result from a greater amount of lean mass or larger flight muscles. This pattern has also been shown in wintering black capped chickadees where males had on average 10.3% more lean mass than females, due to larger skeletal muscles and larger organs (heart, lungs, kidneys, liver, brain, skin) (Petit et al. 2014). Larger muscles in males have also been reported in wintering white-breasted nuthatches *Sitta carolinensis* and house sparrows *Passer domesticus* (Liknes and Swanson 2011). Taken together, our results therefore indicate that for a given body size (and location, see Supplementary material Appendix 1 Fig. A3), female body mass seems to contain a proportionally larger amount of fat. As females are structurally smaller than males, this may be required to support a higher mass-specific metabolic rate for a given set of environmental conditions.

Climate change research indicates that temperate winter conditions are changing rapidly (Williams et al. 2015) and climate models predict that extreme winter weather events will increase in both amplitude and frequency at temperate/polar latitudes, while short-term weather will become more variable (Easterling et al. 2000, Stocker et al. 2013). Quantifying the current level of flexibility for phenotypic traits that may impact fitness during winter is therefore fundamental to assess potential shifts in population dynamics and vulnerability of cold-adapted, temperate wintering species (Aguilar-Kirigin and Naya 2013, Williams et al. 2015). As such, our findings are an important first step in this direction as they help to identify the adjustments that enable wintering species to adapt to future climatic stressors.

Acknowledgements – We thank all banders and volunteers of the Canadian snow bunting network for data collection and ongoing enthusiasm about snow bunting research. A special thanks to the following banders whose data were used for the analyses of this paper (alphabetical order): Simon Duval, Liette Fortier, Nancy Furber, Gay Gruner, David Lamble, Rick Ludkin, Theresa Mckenzie. Fergus Nicoll. We also thank Alain Caron and Nicolas Casajus for their help with statistical analyses.
Funding – M.-P. Laplante received scholarships from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Fond de recherche du Québec - Nature et technologies (FRQNT). This research was supported by NSERC Discovery grants to F.V. and O.P.L. as well as Canada Research Chair funding to O.P.L.

References

Aguilar-Kirigin, A. J. and Naya, D. E. 2013. Latitudinal patterns in phenotypic plasticity: the case of seasonal flexibility in lizards' fat body size. – Oecologia 173: 745–752.

Balen, J. van 1967. The significance of variations in body weight and wing length in the great tit, *Parus major*. – Ardea 55: 1–59.

Barton, K. 2009. MuMIn: multi-model inference. – R package ver. 1.0.0, <http://r-forge.r-project. org/projects/mumin/>.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bednekoff, P. A. and Houston, A. I. 1994. Optimizing fat reserves over the entire winter: a dynamic model. – Oikos 71: 408–415.

Bednekoff, P. A. and Krebs, J. R. 1995. Great tit fat reserves: effects of changing and unpredictable feeding day length. – Funct. Ecol. 9: 457–462.

Bednekoff, P. A., Biebach, H. and Krebs, J. 1994. Great tit fat reserves under unpredictable temperatures. – J. Avian Biol. 25: 156–160.

Best, L. B., Campa III, H., Kemp, K. E., Robel, R. J., Ryan, M. R., Savidge, J. A., Weeks, H. P. and Winterstein, S. R. 1998. Avian abundance in CRP and crop fields during winter in the midwest. – Am. Midl. Nat. 139: 311–324.

Blem, C. R. 1976. Patterns of lipid storage and utilization in birds. – Am. Zool. 16: 671–684.

Blem, C. R. 1990. Avian energy storage. – In: Power, D. M. (ed.), Current ornithology. Plenum Press, pp. 59–113.

Blem, C. R. and Shelor, M. H. 1986. Multiple regression analyses of midwinter fattening of the white-throated sparrow. – Can. J. Zool. 64: 2405–2411.

Bonter, D. N., Zuckerberg, B., Sedgwick, C. W. and Hochachka, W. M. 2013. Daily foraging patterns in free-living birds: exploring the predation-starvation trade-off. – Proc. R. Soc. B 280: 20123087.

Brasnett, B. 1999. A global analysis of snow depth for numerical weather prediction. – J. Appl. Meteorol. 38: 726–740.

Brodin, A. 2001. Mass-dependent predation and metabolic expenditure in wintering birds: is there a trade-off between different forms of predation? – Anim. Behav. 62: 993–999.

Brodin, A. 2007. Theoretical models of adaptive energy management in small wintering birds. – Phil. Trans. R. Soc. B 362: 1857–1871.

Broggi, J., Koivula, K., Lahti, K. and Orell, M. 2003. Seasonality in daily body mass variation in a hoarding boreal passerine. – Oecologia 137: 627–633.

Brown, R. and Brasnett, B. 2010. Canadian meteorological centre (CMC) daily snow depth analysis data, ver. 1.

Carey, C. 2012. Avian energetics and nutritional ecology. – Springer.

Carey, C. and Dawson, W. R. 1999. A search for environmental cues used by birds in survival of cold winters. – In: Nolan, V. Jr et al. (eds), Current ornithology. Vol. 15. Springer, pp. 1–31.

Caswell, H. 1983. Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. – Am. Zool. 23: 35–46.

Cavieres, G. and Sabat, P. 2008. Geographic variation in the response to thermal acclimation in rufous-collared sparrows: are physiological flexibility and environmental heterogeneity correlated? – Funct. Ecol. 22: 509–515.

Chatterjee, S. and Price, B. 1991. Regression analysis by example. – Wiley.

Clark, C. W. and Ekman, J. 1995. Dominant and subordinate fattening strategies: a dynamic game. – Oikos 72: 205–212.

Cooper, S. J. 2000. Seasonal energetics of mountain chickadees and juniper titmice. – Condor 102: 635–644.

Cuthill, I. C. and Houston, A. L. 1997. Managing time and energy. – In: Krebs, J. R. and Davies, N. B. (eds), Behavioural ecology. Blackwell Scientific, pp. 97–120.

Dawson, W. R. and Marsh, R. L. 1986. Winter fattening in the American goldfinch and the possible role of temperature in its regulation. – Physiol. Zool. 59: 357–368.

Deser, C., Knutti, R., Solomon, S. and Phillips, A. S. 2012. Communication of the role of natural variability in future North American climate. – Nat. Clim. Change 2: 775–779.

Dietz, M. W., Piersma, T., Hedenström, A. and Brugge, M. 2007. Intraspecific variation in avian pectoral muscle mass: constraints on maintaining manoeuvrability with increasing body mass. – Funct. Ecol. 21: 317–326.

Dunn, E. H. 2003. Recommendations for fat scoring. – North Am. Bird Bander 28: 58–63.

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R. and Mearns, L. O. 2000. Climate extremes: observations, modeling and impacts. – Science 289: 2068–2074.

Ekman, J. B. and Hake, M. K. 1990. Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris L.*) during periods of unpredictable foraging success. – Behav. Ecol. 1: 62–67.

Ekman, J. B. and Lilliendahl, K. 1993. Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. – Behav. Ecol. 4: 232–238.

Ficken, M. S., Weise, C. M. and Popp, J. W. 1990. Dominance rank and resource access in winter flocks of black-capped chickadees. – Wilson Bull. 102: 623–633.

Fox, J. and Weisberg, S. 2010. An R companion to applied regression. – Sage Publications.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. – Stat. Med. 27: 2865–2873.

Gelman, A. and Su, Y.-S. 2008. arm: data analysis using regression and multilevel/hierarchical models. – R package, <https://cran.r-project.org/web/packages/arm/index.html>.

Goławski, A., Polakowski, M., Filimowski, P., Stępniewska, K., Stępniewski, K., Kiljan, G. and Kilon, D. 2015. Factors influencing the fat load variation in three wintering bird species under stable food access conditions. – J. Ethol. 33: 205–211.

Gosler, A. G. 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. – J. Anim. Ecol. 65: 1–17.

Gosler, A. G. 2002. Strategy and constraint in the winter fattening response to temperature in the great tit *Parus major*. – J. Anim. Ecol. 71: 771–779.

Grueber, C. E., Nakagawa, S., Laws, R. J. and Jamieson, I. G. 2011. Multimodel inference in ecology and evolution: challenges and solutions. – J. Evol. Biol. 24: 699–711.

Guglielmo, C. G., McGuire, L. P., Gerson, A. R. and Seewagen, C. L. 2011. Simple, rapid, and non-invasive measurement of fat, lean, and total water masses of live birds using quantitative magnetic resonance. – J. Ornithol. 152: 75.

Haftorn, S. 1989. Seasonal and diurnal body weight variations in titmice, based on analyses of individual birds. – Wilson Bull. 101: 217–235.

Hair, J. F. 1998. Multivariate data analysis. – Prentice Hall.

Hedenström, A. 1992. Flight performance in relation to fuel load in birds. – J. Theor. Biol. 158: 535–537.

Heinrich, B. 2009. Winter world: the ingenuity of animal survival. – Harper Perennial.

Houston, A. I. and McNamara, J. M. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. – Ornis Scand. 24: 205–219.

Houston, A. I., McNamara, J. M. and Hutchinson, J. M. 1993. General results concerning the trade-off between gaining energy and avoiding predation. – Phil. Trans. R. Soc. B 341: 375–397.

Karpouzos, H., Hernandez, A. M., MacDougall-Shackleton, E. A. and MacDougall-Shackleton, S. A. 2005. Effects of day-length and food availability on food caching, mass and fat reserves in black-capped chickadees (*Poecile atricapillus*). – Physiol. Behav. 84: 465–469.

Kelly, J. P., Warnock, N., Page, G. W. and Weathers, W. W. 2002. Effects of weather on daily body mass regulation in wintering dunlin. – J. Exp. Biol. 205: 109–120.

King, J. R. 1972. Adaptive periodic fat storage by birds. – In: Vous, K. H. (ed.), Proc. 15th Intern. Ornithol. Congr. Plenum Press, pp. 200–217.

Krams, I., Cirule, D., Suraka, V., Krama, T., Rantala, M. J. and Ramey, G. 2010. Fattening strategies of wintering great tits support the optimal body mass hypothesis under conditions of extremely low ambient temperature. – Funct. Ecol. 24: 172–177.

Krementz, D. G. and Pendleton, G. W. 1990. Fat scoring: sources of variability. – Condor 92: 500–507.

Laplante, M.-P., McKinnon, E. A., Love, O. P. and Vézina, F. 2019. Data from: Flexible response to short-term weather in a cold-adapted songbird. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.f7h4614>.

Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. – Methods Ecol. Evol. 7: 573–579.

Lehikoinen, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. – Ornis Scand. 18: 216–226.

Liknes, E. T. and Swanson, D. L. 2011. Phenotypic flexibility of body composition associated with seasonal acclimatization in passerine birds. – J. Therm. Biol. 36: 363–370.

Lilliendahl, K. 1997. The effect of predator presence on body mass in captive greenfinches. – Anim. Behav. 53: 75–81.

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. – Ecology 67: 377–385.

Liu, J. and Li, M. 2005. Phenotypic flexibility of metabolic rate and organ masses among tree sparrows *Passer montanus* in seasonal acclimatization. – Acta Zool. Sin. 52: 469–477.

Macdonald, C. A., McKinnon, E. A., Gilchrist, H. G. and Love, O. P. 2015. Cold tolerance, and not earlier arrival on breeding grounds, explains why males winter further north in an Arctic-breeding songbird. – J. Avian Biol. 47: 7–15.

Macleod, R., Barnett, P., Clark, J. A. and Cresswell, W. 2005. Body mass change strategies in blackbirds *Turdus merula*: the starvation–predation risk trade-off. – J. Anim. Ecol. 74: 292–302.

Mandin, C. and Vézina, F. 2012. Daily variation in markers of nutritional condition in wintering black-capped chickadees *Poecile atricapillus*. – Ibis 154: 791–802.

McKinnon, E. A., Macdonald, C. M., Gilchrist, H. G. and Love, O. P. 2016. Spring and fall migration phenology of an Arctic-breeding passerine. – J. Ornithol. 157: 1–13.

McNamara, J. M. and Houston, A. I. 1990. The value of fat reserves and the tradeoff between starvation and predation. – Acta Biotheor. 38: 37–61.

Menard, S. W. 1995. Applied logistic regression analysis. – Sage Publications.

Metcalfe, N. B. and Ure, S. E. 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. – Proc. R. Soc. B 261: 395–400.

Montgomerie, R. and Lyon, B. 2011. Snow bunting (*Plectrophenax nivalis)*, ver. 2.0. – In: Poole, A. (ed.), Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA, <https://doi.org/10.2173/bna.198>.

Neter, J., Wasserman, W. and Kutner, M. H. 1989. Applied linear regression models. – Irwin.

Newton, I. 1969. Winter fattening in the bullfinch. – Physiol. Zool. 42: 96–107.

Nolan, V. and Ketterson, E. D. 1983. An analysis of body mass, wing length, and visible fat deposits of dark-eyed Juncos wintering at different latitudes. – Wilson Bull. 95: 603–620.

Petit, M., Lewden, A. and Vézina, F. 2013. Intra-seasonal flexibility in avian metabolic performance highlights the uncoupling of basal metabolic rate and thermogenic capacity. – PLoS One 8: e68292.

Petit, M., Lewden, A. and Vézina, F. 2014. How does flexibility in body composition relate to seasonal changes in metabolic performance in a small passerine wintering at northern latitude? – Physiol. Biochem. Zool. 87: 539–549.

Polo, V., Carrascal, L. M. and Metcalfe, N. B. 2007. The effects of latitude and day length on fattening strategies of wintering coal tits *Periparus ater*: a field study and aviary experiment. – J. Anim. Ecol. 76: 866–872.

Pravosudov, V. V. and Grubb, T. C. 1997. Energy management in passerine birds during the nonbreeding season. – In: Nolan, V. et al. (eds), Current ornithology. Springer, pp. 189–234.

Pyle, P. 1997. Identification guide to North American birds. Part 1. – Slate Creek Press, Bolinas.

Raudenbush, S. W. and Bryk, A. S. 2001. Hierarchical linear models: applications and data analysis methods. – Sage Publications.

Rogers, C. M. 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? – Ecology 68: 1051–1061.

Rogers, C. M. 1991. An evaluation of the method of estimating body fat in birds by quantifying visible subcutaneous fat (una evaluación del método para estimar la cantidad de grasa en aves, mediante la cuantificación de la grasa subcutanea visible). – J. Field Ornithol. 62: 349–356.

Rogers, C. M. and Reed, A. K. 2003. Does avian winter fat storage integrate temperature and resource conditions? A long-term study. – J. Avian Biol. 34: 112–118.

Scholander, P. F., Hock, R., Walters, V. and Irving, L. 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. – Biol. Bull. 99: 259–271.

Smith, R. D. 1994. Snow buntings Plectrophenax nivalis: the behavioural ecology and site use of an itinerant flock species in the non-breeding season. – PhD thesis, Univ. of Glasgow.

Smith, R. D. and Metcalfe, N. B. 1994. Age, sex and prior site experience have independent effects on the foraging success of wintering snow buntings. – Behaviour 129: 99–111.

Smith, R. D. and Metcalfe, N. B. 1997. Why does dominance decline with age in wintering snow buntings? – Anim. Behav. 53: 313–322.

Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P. M. 2013 (IPCC 2013). Climate change 2013: the physical science basis. contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. – Cambridge Univ. Press, 1535 pp.

Stokke, B. G., Hafstad, I., Rudolfsen, G., Moksnes, A., Møller, A. P., Røskaft, E. and Soler, M. 2008. Predictors of resistance to brood parasitism within and among reed warbler populations. – Behav. Ecol. 19: 612–620.

Swanson, D. L. and Vézina, F. 2015. Environmental, ecological and mechanistic drivers of avian seasonal metabolic flexibility in response to cold winters. – J. Ornithol. 156: 377–388.

Turcotte, Y. and Desrochers, A. 2008. Forest fragmentation and body condition in wintering black-capped chickadees. – Can. J. Zool. 86: 572–581.

Vincent, J. and Bédard, J. 1976. Fat reserves in snow buntings. – Can. J. Zool. 54: 1051–1063.

Waite, T. A. 1992. Winter fattening in gray jays: seasonal, diurnal and climatic correlates. – Ornis Scand. 23: 499–503.

Williams, C. M., Henry, H. A. and Sinclair, B. J. 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. – Biol. Rev. 90: 214–235.

Witter, M. S. and Cuthill, I. C. 1993. The ecological costs of avian fat storage. – Phil. Trans. R. Soc. B. 340: 73–92.

Zhang, D. 2017. rsq: R-Squared and related measures. – R package ver. 1.0, <http://CRAN.R-project.org/package=rsq>.

Zheng, W. H., Li, M., Liu, J. S. and Shao, S. L. 2008. Seasonal acclimatization of metabolism in Eurasian tree sparrows (*Passer montanus*). – Comp. Biochem. Physiol. A. 151: 519–525.

Supplementary material (Appendix JAV-01766 at <www.avianbiology.org/appendix/jav-01766>). Appendix 1.