

Short Communication

Winter feeding influences the cost of living in boreal passerines

 JULI BROGGI,*¹  ESA HOHTOLA² & KARI KOIVULA²
¹*Estación Biológica de Doñana (CSIC), Av. Américo Vespucio 26, Seville, 41092, Spain*
²*Ecology and Genetics Research Unit, University of Oulu, PO Box 3000, Oulu, FIN-90014, Finland*

The plastic regulation of internal energy reserves is acknowledged as the main adaptive response to winter conditions of resident small birds in northern latitudes, a strategy that may be altered whenever human-supplemented food is available. We investigated the effects of supplementary feeding on the energy management strategy of two wild passerine species, the Willow Tit *Poecile montanus* and Blue Tit *Cyanistes caeruleus*, wintering in boreal conditions by measuring body mass and the energy cost of living, i.e. basal metabolic rate. Individuals of both species were heavier, larger and exhibited a higher energy cost of living when captured at the feeders than were individuals captured away from feeders. Fed Willow Tits expended more energy in maintenance, although this difference disappeared once mass was accounted for. Conversely, Blue Tits at feeders had higher mass-adjusted energy cost of living, but only at low ambient temperatures. The results indicate that winter feeding has species-specific effects on overall energy management strategy and modifies the response to environmental conditions of wintering passerines.

Keywords: basal metabolic rate, Blue Tit, *Cyanistes caeruleus*, mass-adjusted basal metabolic rate, *Poecile montanus*, whole-animal basal metabolic rate, Willow Tit.

Endotherms wintering at high latitudes struggle to survive as environmental conditions deteriorate at the same time as food availability diminishes. Small birds survive this situation through seasonal acclimatization based on an increased metabolic output to meet thermogenic

demands (Broggi *et al.* 2004), and the enlargement of internal energy reserves (Blem 2000).

The adaptive acquisition and storage of reserves is the main mechanism to maintain energy balance in wintering small birds (Pravosudov & Grubb 1997, Brodin 2007). Body mass (M_b) fluctuations resulting from daily increase and overnight depletion of internal reserves constitute the core of the 'optimal body mass' (OBM) theory of energy management in wintering small birds (Moiron *et al.* 2018). This daily M_b cycle is predicted to widen as temperatures and food predictability decrease (i.e. higher evening M_b and lower morning M_b) (Pravosudov & Grubb 1997).

In addition to internal reserves, wintering small birds save energy through regulation of body temperature and the cost of living (i.e. basal metabolism) as part of their energy management strategy (McKechnie & Lovegrove 2002, Broggi *et al.* 2019). M_b and basal metabolic rate (BMR) are phenotypically integrated traits that are highly and positively related (McNab 1997, Hayes 2001). The interrelation between the two traits varies individually according to tissue composition and proportions, which change with physiological, ecological and environmental conditions (Klaassen & Biebach 1994, Rønning *et al.* 2008, Broggi *et al.* 2019).

Providing supplementary food to wild birds is becoming an increasingly popular human activity which presumably allows individual birds to obtain their optimal energy reserve level more readily (Robb *et al.* 2008). However, winter-feeding may have wider physiological and ecological consequences that only recently have started to be studied (Robb *et al.* 2008). For example, increased food availability and predictability may come at the cost of impoverished diet, higher predation risk and pathogen exposure, with negative fitness consequences (Barea & Watson 2013).

The Blue Tit *Cyanistes caeruleus* and the Willow Tit *Poecile montanus* are two similar small-sized (~ 10 g) species of the family Paridae that are widespread across Europe. The Blue Tit is a temperate species inhabiting deciduous forests and has expanded northwards into boreal regions in recent decades (Valkama *et al.* 2011). Blue Tits at the northern margin of the distribution spend winters mostly near human habitation where, like the Great Tit *Parus major*, they rely on feeders for survival, a habit that presumably explains the successful expansion of both species (Orell 1989). However, in contrast to Great Tits, a fraction of the Blue Tit population persists during winter in the reedbeds and birch forests along the coastline, away from inhabited buildings and feeders (J. Broggi & K. Koivula pers. obs.). The Willow Tit is a highly sedentary forest species that is well adapted to survive winters without the need for human-provided food. Once settled, individuals remain all year round within their territory, where they hoard scattered food-caches for winter survival (Lahti *et al.* 1998).

Corresponding author.
 Email: julibroggi@gmail.com

Additionally, Willow Tits prioritize energy-saving mechanisms, allowing them to buffer the effects of environmental variation in comparison with other temperate species such as the Blue Tit (Broggi *et al.* 2003, 2019). Thus, although the two species have a similar size and face the same thermal challenges, they maintain different seasonal energy management strategies (Broggi *et al.* 2019). However, recapture evidence from both species suggests that whenever individuals find a feeder, they rarely move away from such a steady food source, particularly during cold periods (Lahti *et al.* 1998, Pakanen *et al.* 2018).

Here we studied how permanent access to supplementary food influences M_b and winter BMR in wild Willow and Blue Tit populations in boreal conditions. We hypothesize that feeder users will enjoy an increased food predictability that will affect their optimal reserve level. Further, the overall energy budget will possibly increase, leading to a higher energetic cost of living, measured by BMR. Following the OBM theory, birds at feeders are expected to reduce their M_b and increase their BMR. We expect that proximity to feeders reduces sensitivity to environmental conditions. Further, we expect the two species to differ in their response, as boreal specialists such as the Willow Tit should be better adapted to withstand local conditions compared with temperate species such as the Blue Tit, and thus be less affected by food supplementation.

METHODS

Study area and experimental approach

We analysed M_b and BMR of 61 wintering Blue and Willow Tit individuals in the Oulu region, Finland (65°N, 25°30'E) between 2003 and 2010. We tested the effect of artificial food supplementation by comparing birds of both species from permanently fed and non-fed areas (Fig. 1). In the fed area, birds were captured by funnel traps baited with unhusked peanuts near the Oulu University campus (19 Blue Tits and 23 Willow Tits). Data from these fed birds were selected from a larger dataset that has been already published to match in time (year and season) with the non-fed birds (see below) (Broggi *et al.* 2019). Supplementary food was provided near the University campus from early September to late March, and feeders were refilled on a weekly basis to ensure a permanent supply. The Oulu study area is a forest mosaic of mixed tree species of different ages dominated by conifers *Pinus sylvestris* and *Picea abies* and diverse birch *Betula* sp. species. Average winter temperatures fall below -10 °C with a permanent snow cover that remains for 5 months. Birds from the non-fed areas were captured with mist-nets by luring them with sound recordings, and small feeders were

installed on the same capture day (six Blue Tits and 13 Willow Tits). Non-fed Blue Tits were trapped in coastal areas c.40 km south of Oulu, in an area of reedbeds and coastal birch forest away from any urban centres (Fig. 1). The thick snow layer (> 2 m) and frozen sea that characterizes the area from November until late April prevents any access to the summer cottages present and ensures that there is no supplementary feeding during winter months. Non-fed Willow Tits were captured in the Oulu study area to the north of the town (Fig. 1), where resident flocks remain faithful to their territories after settling down in early winter as first-year birds (Koivula & Orell 1988).

The different capture methods did not affect recapture probability and did not bias the samples obtained, as shown by a subsample of individuals trapped with tape lures and mist-nets at the fed area (Broggi 2006, pp 21–28; J. Broggi in prep.). All birds were trapped in the afternoon between midday and 14:00 h, measured for biometric variables, and immediately transported to the University laboratory. Birds were transported in ringing bags and then maintained in individual cages for a short period (< 2 h) of time before night-time measurements. Cages consisted of small (0.3 m^3) metallic mesh cubes covered with a blind fabric to minimize stress. *Ad libitum* food (unhusked peanuts and mealworms) and water supply were provided before BMR measurements were taken (see below). Time spent in the cages did not affect BMR measurements (J. Broggi unpubl. data).

Metabolic measurements

BMR is defined as the average minimal oxygen consumption under post-absorptive digestive conditions during the resting phase of the daily cycle of non-growing, non-reproductive animals at thermoneutrality (McNab 1997). BMR is the most widely used energetic measure in biological and medical studies and constitutes a major part of the daily energy expenditure in wintering birds (Broggi *et al.* 2004), potentially affecting overwinter survival (Nilsson & Nilsson 2016). Oxygen consumption of (up to) four individuals each night was used to measure BMR in an open-circuit respirometer in a dark climate chamber at a constant temperature of 25 °C, within the thermoneutral zone of the species (Reinertsen & Haftorn 1986). In brief, outdoor dry air was pushed through four independent mass-flow controllers (FMA-A2407; Omega Engineering, Inc., Norwalk, CT, USA) at 300 mL/min into plexiglass metabolic chambers (1.6 L) containing each individual bird. Constantly flowing incoming and outgoing air was scrubbed for CO₂ and H₂O, with soda-lime and silica scrubbers, then directed through a multiplexer that sent air from each channel in bouts of 12 min to the oxygen analyser (S-3A; Ametek, Pittsburgh, PA, USA). Each cycle lasted an hour and included

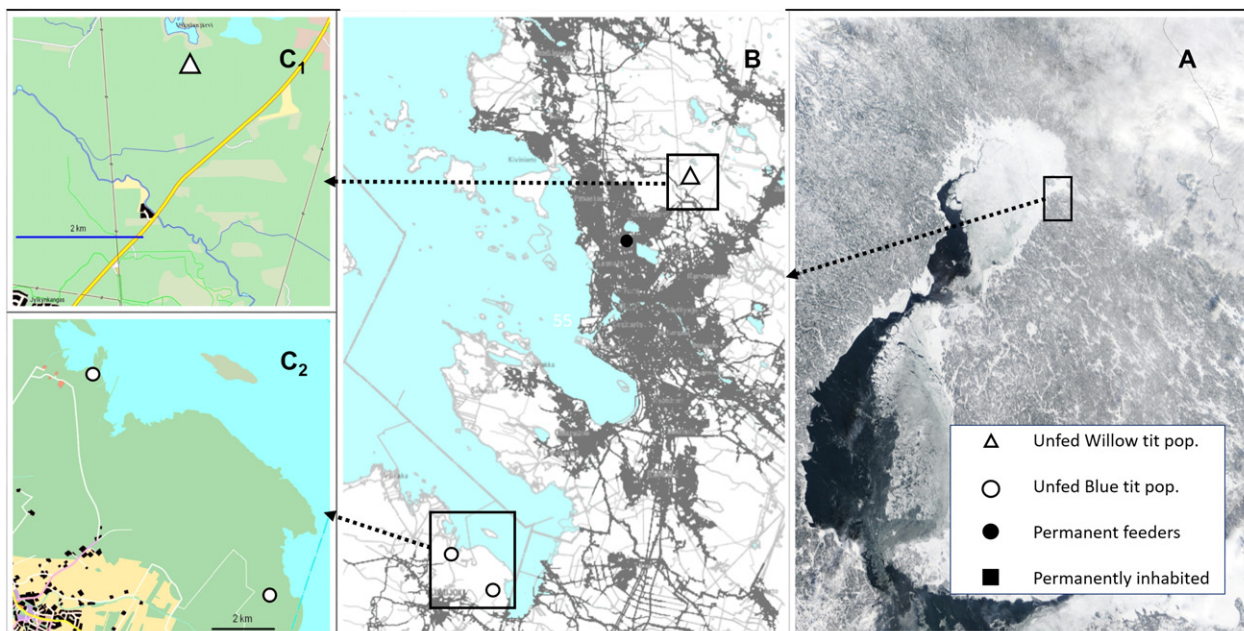


Figure 1. Maps of the study area at three different scales. Satellite picture from the Bothnian bay in winter (A), showing sea ice. Map of the Oulu region with the different trapping localities (B), and the human-inhabited areas in dark. The non-fed study areas for Willow Tit *Poecile montanus* (C₁) and Blue Tit *Cyanistes caeruleus* (C₂) with the corresponding scale, showing the distance to permanently inhabited houses (in black) that indicates the presence of potential feeders. Different trapping locations are indicated with different symbols. Permanent feeders are marked by full circles; non-fed localities for Willow Tit are marked by open triangles and for Blue Tit by open circles. [Colour figure can be viewed at wileyonlinelibrary.com]

a fifth channel with reference air to control for the analyser bias. Recorded data were visually inspected, and the lowest 5 min of steady measurements were converted to mL O₂/min following Hill (1972). BMR measurements were invariably taken between midnight and 04:00 h, ensuring the post-absorptive state of all individuals. After the measurement night, birds were released at the point of capture.

Statistical analyses

We used general linear models to explain variation in M_b , BMR and mass-adjusted BMR. Mass-adjusted BMR was studied by analysing BMR as the dependent variable, with M_b fitted as a covariate. Whole-animal and mass-adjusted BMR can be considered different traits that provide information on different scales of the individual energy expenditure (Hayes 2001). Whole-animal BMR reflects the overall energy cost of maintenance of an individual, and variation can be interpreted as a general increase in the overall size with a concomitant increase in the energy cost of living, which may sometimes be paralleled by changes in organ sizes and/or the proportion of tissues with different metabolic activity (Petit *et al.* 2014). Mass-adjusted BMR is the energetic

cost per unit mass, and variation probably involves a substantial change in the metabolic intensity resulting from differences in tissue proportions that allow the metabolic comparison of individuals of different weight (Mueller & Diamond 2001, Rønning *et al.* 2008). Individual variables included age (first winter or older) and sex as categorical predictors. Willow Tits during the non-breeding season can be sexed reliably through sexual dimorphism in wing length (Koivula & Orell 1988), and thus only tarsus and wing length (mm) were considered as continuous predictors of body size and sex. Environmental variables considered were day of capture (1 October = 1), winter of study (2003–2004 = 1) and minimum temperature (T_{min}) on capture day (in °C). The quadratic component of day of capture was included to test for non-linear effects of date, which reflect photoperiodic cyclicity over the non-breeding season. Each variable was tested individually together with treatment (supplementary-fed vs. non-fed) as a fixed factor and their interaction in all analyses, except for the analyses of mass-adjusted BMR, where M_b was included as covariate. Models with significant variables are presented (Table 1) together with the F , df and P -values of the last predictor incorporated. Parameter estimates \pm se are provided for significant continuous

predictors. All P -values are two-tailed. All continuous variables fulfilled the requirements of normality.

RESULTS

Blue Tits at feeders were heavier than birds from non-fed areas after sex and size were accounted for (Fed: $12.103 \text{ g} \pm 0.147$ vs. Non-fed: $10.928 \text{ g} \pm 0.263$; $F_{1,20} = 15.43$; $P < 0.001$; Fig. 2). However, such differences in M_b were not reflected in either BMR or mass-adjusted BMR (Table 1; Fig. 2). Blue Tit males were heavier than females, and heavier Blue Tits had longer wing and tarsus length (Table 1). Otherwise, M_b was not related to age or any of the environmental parameters considered (Table 1). These patterns persisted between fed and non-fed areas, as none of the interactions between these variables and treatment were significant (all $P > 0.05$). However, BMR was negatively influenced by T_{\min} , a pattern that differed between fed and non-fed treatments for mass-adjusted BMR, while all the other variables remained non-significant (all $P > 0.05$; Table 1). Fed Blue Tits showed a higher mass-adjusted BMR with decreasing T_{\min} , whereas the effect was not significant in non-fed birds (Table 1; Fig. 3).

Willow Tits were heavier and had a higher BMR at feeders (Table 1; Fig. 2). However, mass-adjusted BMR did not differ between fed and non-fed areas (Table 1; Fig. 2). Patterns of variation in M_b , BMR and mass-adjusted BMR were independent of any size or age differences, as shown by non-significant interactions between

these variables and treatment (all $P > 0.05$). Willow Tit age and size were related to M_b but not to BMR or mass-adjusted BMR. Juvenile Willow Tits were heavier than adults, and heavier Willow Tits had longer wings (Table 1). Willow Tit M_b , BMR and mass-adjusted BMR were not related to T_{\min} or year of study (Table 1, Fig. 3). However, BMR and mass-adjusted BMR were non-linearly related to capture date, with a drop in mid-winter (Table 1; Fig. 3). None of these seasonal patterns differed between experimental areas, as shown by non-significant interactions with treatment (all $P > 0.05$).

DISCUSSION

Small birds wintering in boreal regions respond to supplementary feeding with substantial physiological changes involving body mass and energy expenditure. Both Blue and Willow Tits had higher M_b when captured at the feeders (+6.29% and +4.48%, respectively). Additionally, access to feeders promoted increased BMR in Willow Tits (+7.78%), whereas Blue Tits exhibited a conditional response to the immediate environmental conditions. Blue Tits with access to feeders had higher metabolic intensity (i.e. mass-adjusted BMR) when minimum temperatures dropped. Winter supplementary feeding affects the energy strategy and response to environmental conditions of the two studied species differently.

Body mass was higher in both species studied as a response to winter food supplementation, suggesting

Table 1. Results from the general linear models of Willow Tit *Poecile montanus* and Blue Tit *Cyanistes caeruleus* body mass (g) (M_b), basal metabolic rate (mL O_2 /min) (BMR) and mass-adjusted BMR (BMR_{mass}) as dependent variables.

Species	Dependent Variable	Estimate	F	df	P	
Willow Tit	Body mass	TR	Fed: 11.817 ± 0.125 vs. Non-fed: 11.289 ± 0.166	6.45	1,34	0.016
		TR + Age	Jv: 11.733 ± 0.119 vs. Ad: 11.242 ± 0.148	4.27	1,33	0.012
		TR + Wing	0.149 ± 0.047	9.93	1,33	0.004
	BMR	TR	Fed: 0.903 ± 0.166 vs. Non-fed: 0.825 ± 0.028	4.76	1,34	0.036
		TR + Date ²	$< 0.001 \pm < 0.001$	5.77	1,32	0.022
		TR + M_b	0.069 ± 0.027	6.57	1,33	0.015
Blue Tit	Body mass	TR + Sex	Male: 12.112 ± 0.168 vs. Female: 10.879 ± 0.233	20.25	1,20	<0.001
		TR + Wing	0.217 ± 0.069	9.85	1,20	0.005
		TR + Tarsus	0.597 ± 0.172	12.08	1,20	0.002
	BMR	TR + T_{\min}	$< -0.005 \pm 0.002$	4.58	1,20	0.045
		TR + M_b	0.051 ± 0.023	4.75	1,22	0.004
		TR + $M_b + T_{\min}$	$< -0.005 \pm 0.002$	5.98	1,19	0.024
BMR _{mass}	TR + $M_b + TR * T_{\min}$	Fed: -0.006 ± 0.002 vs. Non-fed: 0.015 ± 0.010	4.27	1,18	0.053	

BMR_{mass} was analysed by setting BMR as the dependent variable and considering M_b as a covariate. All models included treatment (TR; fed vs. non-fed) as a fixed factor. Whenever a variable was found to be significant, the interaction with treatment was analysed. Predictors from the models are shown, together with the corresponding F -values, df and P -values, and parameter estimates \pm se. Significant terms are presented in bold. TR, Treatment (fed vs. non-fed); Tarsus, tarsus length (mm); Wing, wing length (mm); Date, calendar day (1 October = 1); Winter, winter of study (2003–2004 = 1); T_{\min} , minimum temperature ($^{\circ}\text{C}$); +, term included in the model; *, interaction.

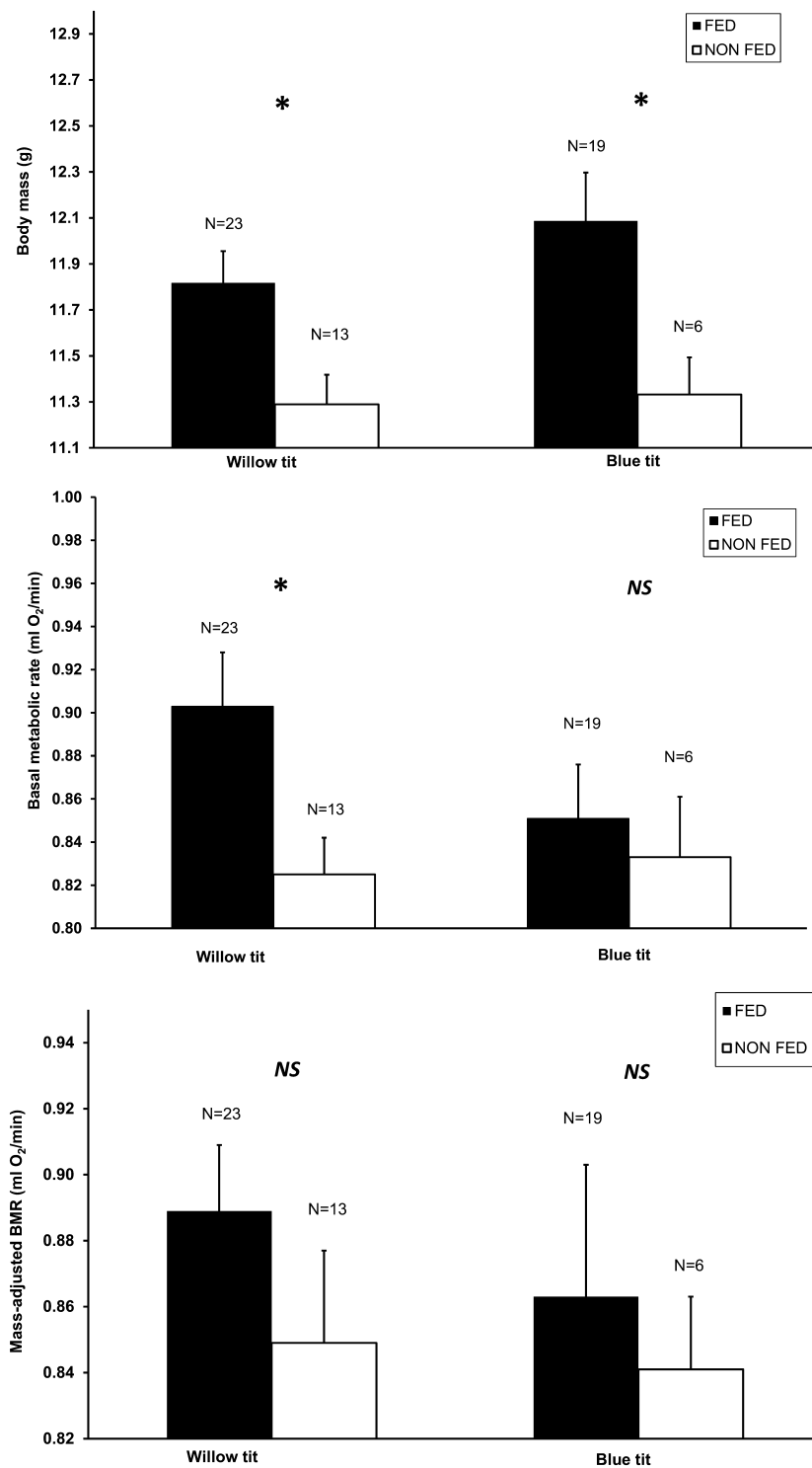


Figure 2. Mean body mass (g), basal metabolic rate (mL O₂/min) and mass-adjusted basal metabolic rate (mL O₂/min) for Willow Tits *Poecile montanus* and Blue Tits *Cyanistes caeruleus* from fed (black columns) and non-fed (open columns) areas. Least-square means from initial models are presented with the corresponding se. *, Statistically significant difference where $P < 0.05$ and NS for non-significant difference between treatments. Sample sizes for each group are provided.

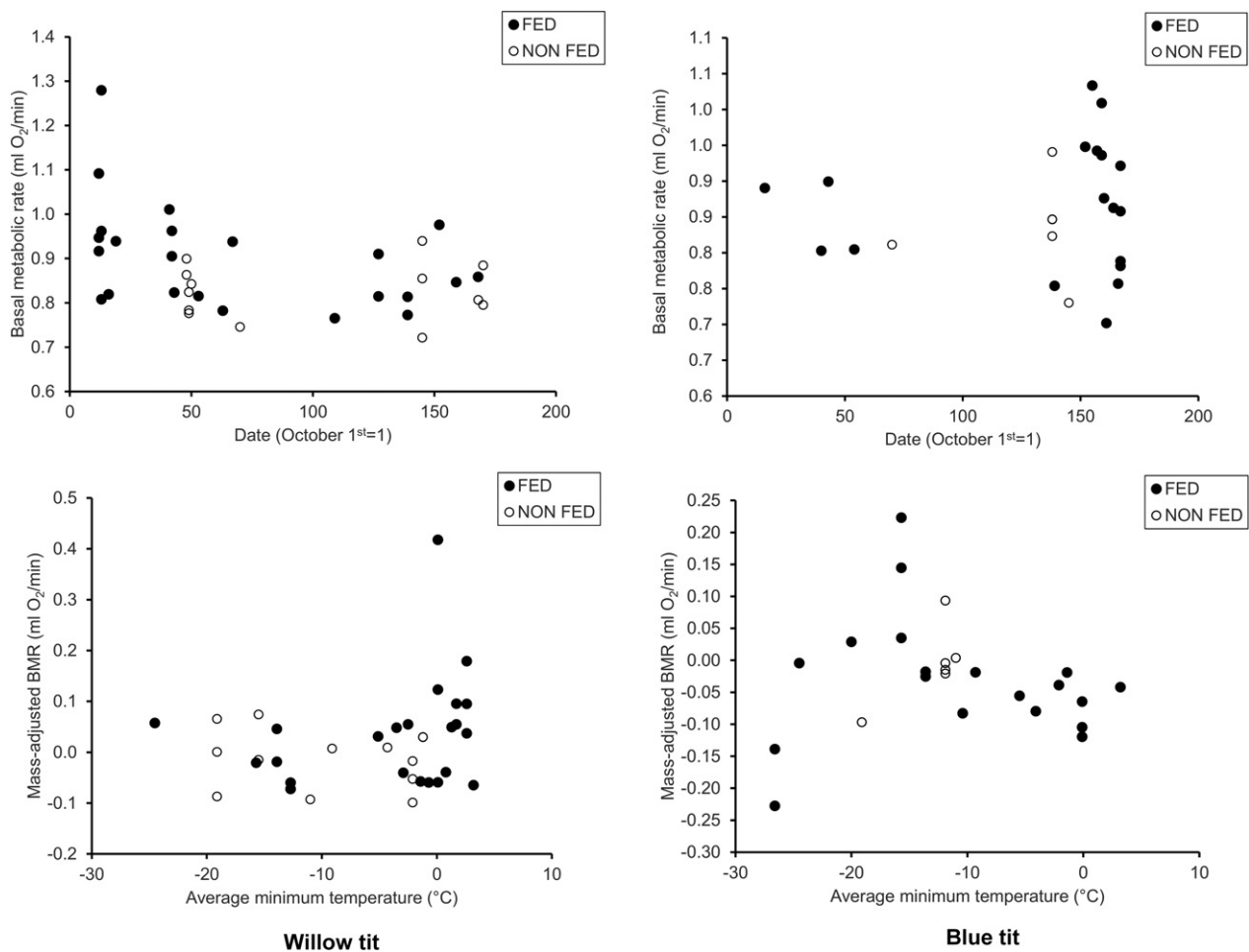


Figure 3. Mass-adjusted basal metabolic rate (mL O₂/min) and basal metabolic rate (mL O₂/min) in relation to average minimum temperature (°C) and date (1 October = 1) of measurement of Willow Tits *Poecile montanus* and Blue Tits *Cyanistes caeruleus* from fed (full black circles) and non-fed (open circles) areas.

that the studied populations may be food-constrained. Further, access to feeders did not promote a reduction in M_b , as predicted by the OBM, but vice versa (Brodin 2007, Moiron *et al.* 2018). Even well-adapted boreal species seem to make use of extra food whenever available, suggesting that local conditions are extreme and that energy-saving mechanisms are not cost-free (Pravosudov & Grubb 1997).

BMR was higher as a result of access to feeders only in Willow Tits, a response probably linked to the higher M_b . Whenever more food is ingested, a larger processing capacity is required, which may lead to increased size in digestive and cardiopulmonary organs (Mueller & Diamond 2001, Nilsson 2002, Petit *et al.* 2014). Blue Tits did not change their overall energy budget, as BMR remained practically unaffected by the presence of feeders. However, Blue Tits at the feeders responded to the environmental conditions by increasing their metabolic

intensity (i.e. mass-adjusted BMR) when T_{\min} decreased. Changes in mass-adjusted BMR or just M_b would be indicative of a substantial tissue reorganization (Hayes 2001) and increased internal reserves, respectively (Klaassen & Biebach 1994). These results suggest that Blue Tits react to an immediate environmental challenge only when food availability is guaranteed.

Boreal and temperate specialist species such as Blue and Willow Tits differ in their metabolic response to food supplementation rather than in body mass, suggesting a relevant role of energy expenditure over internal reserves in energy management in these species, in line with previous studies (Broggi *et al.* 2019). The changes in metabolism in both species suggest that the variation in M_b not only resulted from regulation of internal reserves but is also affected by other mechanisms such as changes in organ sizes and tissue composition (Petit *et al.* 2014).

Here we show that supplementary feeding of wild wintering birds promotes a higher M_b , as a result of an improved food availability, which is also paralleled by changes in the energy cost of living and its response to environmental conditions. These results highlight the multifaceted nature of winter energy management in small passerines by showing that changes in body mass are not only the result of internal reserve variation (Broggi *et al.* 2019). Winter supplementary feeding has species-specific physiological and ecological implications, which certainly need to be addressed to comprehend fully the impact on wild animal populations.

We are in debt to numerous field assistants and staff from the Oulu University Research Facility who provided logistic and technical support and field assistance. Jan Åke Nilsson provided valuable comments on earlier drafts of the manuscript. The manuscript was improved by the comments of Simon Butler and two anonymous referees.

J.B. has been funded by the Andalucía Talent Hub Program launched by the Andalusian Knowledge Agency, co-funded by the European Union's Seventh Framework Program, Marie Skłodowska-Curie actions (COFUND – Grant Agreement no. 291780) and the Junta de Andalucía. The study was supported by the Academy of Finland project nos. 102286 and 47195, and the Thule Institute of the University of Oulu (E.H.).

CONFLICT OF INTEREST

We have no competing interests.

AUTHOR CONTRIBUTIONS

Juli Broggi: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (equal); Resources (supporting); Software (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Esa Hohtola:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Software (supporting); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing-review & editing (equal). **Kari Koivula:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (supporting); Resources (supporting); Supervision (equal); Visualization (equal); Writing-review & editing (equal).

ETHICS

All procedures were conducted in agreement with the local ethics committee (Finnish National Animal Experiment Board).

DATA AVAILABILITY STATEMENT

Data will be provided by the author upon reasonable request. Data are available at: <http://hdl.handle.net/10261/211239>

REFERENCES

- Barea, L.P. & Watson, D.M.** 2013. Trapped between popular fruit and preferred nest location – cafeterias are poor places to raise a family. *Funct. Ecol.* **27**: 766–774.
- Blem, C.R.** 2000. Energy balance. In Sturkie, P.D. & Whittow, G.C. (eds) *Sturkie's Avian Physiology*. 327–341. San Diego, CA: Academic Press.
- Brodin, A.** 2007. Theoretical models of adaptive energy management in small wintering birds. *Philos. Trans. R. Soc. B* **362**: 1857–1871.
- Broggi, J.** 2006. Patterns of variation in energy management in wintering tits (Paridae). *Acta Universitatis Oulensis A* **467**, pp(21–28).
- Broggi, J., Koivula, K., Lahti, K. & Orell, M.** 2003. Seasonality in daily body mass variation in a hoarding boreal passerine. *Oecologia* **137**: 627–633.
- Broggi, J., Orell, M., Hohtola, E. & Nilsson, J.-Å.** 2004. Metabolic response to temperature variation in the Great Tit: an interpopulation comparison. *J. Anim. Ecol.* **73**: 967–972.
- Broggi, J., Nilsson, J.F., Koivula, K., Hohtola, E. & Nilsson, J.-Å.** 2019. Mass or pace? Seasonal energy management in wintering boreal passerines. *Oecologia* **189**: 339–351.
- Hayes, J.P.** 2001. Mass-specific and whole-animal metabolism are not the same concept. *Physiol. Biochem. Zool.* **74**: 147–150.
- Hill, R.W.** 1972. Determination of oxygen consumption by use of paramagnetic oxygen analyzer. *J. Appl. Physiol.* **33**: 261–263.
- Klaassen, M. & Biebach, H.** 1994. Energetics of fattening and starvation in the long-distance migratory garden warbler, *Sylvia borin*, during the migratory phase. *J. Comp. Physiol. B* **164**: 362–371.
- Koivula, K. & Orell, M.** 1988. Social rank and winter survival in the Willow Tit *Parus montanus*. *Orn. Fenn.* **65**: 114–120.
- Lahti, K., Orell, M., Rytönen, S. & Koivula, K.** 1998. Time and food dependence in Willow Tit winter survival. *Ecology* **79**: 2904–2916.
- McKechnie, A.E. & Lovegrove, B.G.** 2002. Avian facultative hypothermic responses: a review. *Condor* **104**: 705–724.
- McNab, B.K.** 1997. On the utility of uniformity in the definition of basal rate of metabolism. *Physiol. Zool.* **70**: 718–720.
- Moiron, M., Mathot, K.J. & Dingemans, N.J.** 2018. To eat and not be eaten: diurnal mass gain and foraging strategies in wintering Great Tits. *Proc. R. Soc. B* **285**: 20172868.
- Mueller, P. & Diamond, J.M.** 2001. Metabolic rate and environmental productivity: well-provisioned animals evolved

- to run and idle fast. *Proc. Natl. Acad. Sci. USA* **98**: 12550–12554.
- Nilsson, J.-Å.** 2002. Metabolic consequences of hard work. *Proc. R. Soc. B* **269**: 1735–1739.
- Nilsson, J.F. & Nilsson, J.-Å.** 2016. Fluctuating selection on basal metabolic rate. *Ecol. Evol.* **6**: 1197–1202.
- Orell, M.** 1989. Population fluctuations and survival of Great Tits *Parus major* dependent on food supplied by man in winter. *Ibis* **131**: 112–127.
- Pakanen, V.-M., Karvonen, J., Mäkelä, J., Hietaniemi, J.P., Jaakkonen, T., Kaisanlahti, E., Kauppinen, M., Koivula, K., Luukkonen, A., Rytönen, S., Timonen, S., Tolvanen, J., Vatka, E. & Orell, M.** 2018. Cold weather increases winter site fidelity in a group-living passerine. *J. Ornithol.* **159**: 211–219.
- Petit, M., Lewden, A. & 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.
- Pravosudov, V.V. & Grubb, T.C., Jr** 1997. Energy management in passerine birds during the nonbreeding season. A review. *Curr. Ornithol.* **14**: 189–234.
- Reinertsen, R.E. & Haftorn, S.** 1986. Different metabolic strategies of northern birds for nocturnal survival. *J. Comp. Physiol. B* **156**: 655–663.
- Robb, G.N., McDonald, R.A., Chamberlain, D.E. & Bearhop, S.** 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.* **6**: 476–480.
- Rønning, B., Moe, B., Chastel, O., Broggi, J., Langset, M. & Bech, C.** 2008. Metabolic adjustments in breeding female kittiwakes (*Rissa tridactyla*) include changes in kidney metabolic intensity. *J. Comp. Physiol. B* **178**: 779–784.
- Valkama, J., Vepsäläinen, V. & Lehtikoinen, A.** 2011. *The Third Finnish Breeding Bird Atlas*. Helsinki: Finnish Museum of Natural History and Ministry of Environment. <http://atlas3.lintuatlas.fi/english> (ISBN 978-952-10-7145-4)

Received 13 May 2019;
 revision accepted 31 May 2020.
 Associate Editor: Simon Butler.