

Increasing Winter Maximal Metabolic Rate Improves Intrawinter Survival in Small Birds*

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ABSTRACT

Small resident bird species living at northern latitudes increase their metabolism in winter, and this is widely assumed to improve their chances of survival. However, the relationship between winter metabolic performance and survival has yet to be demonstrated. Using capture-mark-recapture, we followed a population of free-living black-capped chickadees (*Poecile atricapillus*) over 3 yr and evaluated their survival probability within and among winters. We also measured the size-independent body mass (M_s), hematocrit (Hct), basal metabolic rate (BMR), and maximal thermogenic capacity (Msum) and investigated how these parameters influenced survival within and among winters. Results showed that survival probability was high and constant both within (0.92) and among (0.96) winters. They also showed that while M_s , Hct, and BMR had no significant influence, sur-

vival was positively related to Msum—following a sigmoid relationship—within but not among winter. Birds expressing an Msum below 1.26 W (i.e., similar to summer levels) had a <50% chance of survival, while birds with an Msum above 1.35 W had at least a 90% chance of surviving through the winter. Our data therefore suggest that black-capped chickadees that are either too slow or unable to adjust their phenotype from summer to winter have little chances of survival and thus that seasonal up-regulation of metabolic performance is highly beneficial. This study is the first to document in an avian system the relationship between thermogenic capacity and winter survival, a proxy of fitness.

Keywords: metabolic rate, BMR, Msum, survival, winter acclimatization, fitness, black-capped chickadee.

Introduction

For resident bird species living at northern latitudes, winters are characterized by low temperatures, reduced food availability, short foraging days, and long nights of fasting (McNamara et al. 1990; Swanson 2010). To face these challenging conditions, small species use several physiological adjustments, such as increases in lean body mass (Williams and Tieleman 2000; Vézina et al. 2006; Petit et al. 2014) and fat reserves (Swanson 1991; Cooper 2002; Petit et al. 2014), elevated basal (BMR) and summit metabolic (Msum) rates (Cooper and Swanson 1994; Petit et al. 2013), as well as increased hematocrit (Hct; Swanson 1990; Petit and Vézina 2014a).

Total body mass (M_b), muscle mass, and fat reserves are proxies of individual condition (Norte et al. 2009). BMR, interpreted here as a measure of physiological maintenance costs, is assumed to vary with changes in size of digestive organs and muscles (Chappell et al. 1999; Williams and Tieleman 2000; Zheng et al. 2008; Liknes and Swanson 2011b; Petit et al. 2014), while Msum, a measure of maximal thermogenic capacity, is mainly related to variations in pectoral muscle size and function (Liknes and Swanson 2011a; Swanson et al. 2013; Petit and Vézina 2014a; Swanson and Vézina 2015). Everything else being equal, Hct—the proportion of red blood cells in total blood—is an indicator of maximal oxygen carrying capacity. It is related to overall metabolic activity (Carpenter 1975; Swanson 1990) and thus varies positively with BMR and Msum (Burness et al. 1998; Petit and Vézina 2014a). Consequently, birds with higher lean mass, larger fat reserves, and higher BMR, Msum, and Hct are assumed to be best equipped to per-

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form in a cold environment and to have better survival relative to birds with lower physiological conditions (Pravosudov and Lucas 2001; Verhulst et al. 2004; Brodin 2007). However, although a positive relationship between these parameters and winter survival is commonly assumed (Swanson and Olmstead 1999; Sears et al. 2006; Nzama et al. 2010; Petit et al. 2013) and has been observed in some small mammals (Jackson et al. 2001; Boratyński et al. 2010), it has yet to be demonstrated in free-living birds (Swanson and Vézina 2015).

With this study, we tested the hypothesis that survival of wintering birds depends on their physiological condition. Assuming that wintering birds increase their lean mass, fat reserves, metabolic performance, and Hct to improve their survival (Swanson and Olmstead 1999; Pravosudov and Lucas 2001) and that high condition reflects high individual quality (Pravosudov and Lucas 2001; Verhulst et al. 2004; Brodin 2007), we expected positive relationships between physiological parameters and survival within winter as well as among years. However, according to the resource allocation principle (Weiner 1992), birds facing challenging conditions, such as winter, could show physiological trade-offs to support their main activities (i.e., thermogenesis and foraging) at the expense of other physiological systems (e.g., immunity, self-maintenance; Wiersma et al. 2004; Ardia and Clotfelter 2007; Buehler et al. 2009). Hence, the energy invested in developing and maintaining the winter phenotype could also potentially compromise winter survival (e.g., by a reduction of self-maintenance) and result in long-term negative carryover effects on fitness (Fretwell 1972; Saino et al. 2004). Consequently, we predicted the relationship between winter phenotype and survival to be nonlinear, with maximal survival reached at an intermediate level of winter performance.

In this study, we applied a capture-mark-recapture (CMR) method to track 231 free-living black-capped chickadees (*Poecile atricapillus*) wintering in eastern Canada from the winter of 2009–2010 to the winter of 2011–2012. We used measurements of M_b , body size, BMR, Msum, and Hct together with recapture and resighting data to investigate, for the first time in birds, the relationship between winter physiological condition and survival both within winter and among years.

Material and Methods

Capture and Handling

Our model species—the black-capped chickadee—is a small (9–14 g), nonmigratory, territorial, philopatric, and short-lived (3 yr) passerine (Weise and Meyer 1979; Smith 1991; Schubert et al. 2007, 2008), which makes it perfectly suited for this study. The study was carried out in the Forêt d'Enseignement et de Recherche Macpès, Quebec, Canada (48°18'N, 68°31'W), from October 2009 to December 2011. To facilitate capture and resighting, six feeding stations were set up during the first year and five stations were added during the second year, with an average distance between stations of 1.9 km. Each station included three metal feeders (Perky-Pet 10-inch Sunflower Seed and Peanut Feeder) filled with black sunflower seeds. Birds

were captured continuously throughout winter from September to March. During captures (between 0800 and 1300 hours), feeders were removed and homemade potter traps (15 cm × 15 cm × 15 cm) baited with seeds were used to catch birds. During the first winter (September 2009–March 2010), we caught 139 birds (cohort 1), of which 72 were resighted in the second year (September 2010–March 2011) and 46 during the third year (November 2011–December 2011). During the second year, we also caught 92 new birds (cohort 2), and 33 were resighted in the third year. Birds caught for the first time were banded with a US Geological Survey numbered metal band and a unique combination of three colored bands for further identification from a distance. At each capture, we collected a blood sample within <10 min by puncturing the brachial vein with a 26-gauge needle. Samples (total blood volume <120 μ L) were kept cold (<4°C but above freezing) in heparanized microcapillary tubes until centrifugation (10 min at 16,000 g) and Hct measurements. After blood sampling, birds were weighed and measured following standardized protocols (length of head plus beak, tarsus, and wing measured; Mandin and Vézina 2012; Petit et al. 2013). We used the shape and wear of the sixth rectrices to determine the age (young or adult) of birds (Pyle et al. 1987). Following these measurements, up to four birds per day were brought to the field station for metabolic trials the same day. Birds were released on their site of capture the next morning around 0800 hours. All bird manipulations were approved by the animal care committee of the Université du Québec à Rimouski (CPA-37-09-68) and have been conducted under scientific and banding permits from Environment Canada–Canadian Wildlife Service.

Respirometry

At the field station, birds were kept in separate cages (39 cm × 43 cm × 31 cm) in a quiet room receiving natural light, with ad lib. access to food (black-oiled sunflower seeds, which allowed black-capped chickadees to maintain their body mass during the duration of captivity [<24 h]; data not shown) and water until metabolic rate measurements. At around 1300 hours, we began to measure the Msum of two birds in parallel, using the instruments and protocol described by Petit et al. (2013). Measurements of the two remaining birds started before 1500 hours. For each sequence, we weighed (± 0.1 g) the birds and recorded their body temperature (T_b) with a thermocouple reader (Omega model HH-25KC, NIST-traceable, Omega, Montreal, Quebec), using a copper-constantan thermocouple inserted into the cloacae approximately 10 mm deep. Then, birds were put in metabolic chambers (effective volume = 1,120 mL) fitted with a perch and a thermistor (Sable Systems UI2 AD converter, Sable Systems, Las Vegas, NV) for chamber temperature measurements. We exposed the birds to helox gas (21% oxygen, 79% helium, average flow rate of 1,109 mL min^{-1}) and measured their oxygen consumption (FoxBox oxygen analyzers, Sable Systems) using a sliding cold exposure protocol (Swanson et al. 1996). This procedure consisted of decreasing ambient temperature by 3°C every 20 min, with trials starting at 0°C. Trials ended when birds

became hypothermic, which was detectable in real time as a steady decline in oxygen consumption for several minutes, time at which we measured the birds' M_b and T_b again. We assumed that a bird had reached its Msum when T_b after a trial was $\leq 38^\circ\text{C}$ (Cooper and Gessaman 2005; mean T_b after Msum = $33.4^\circ \pm 0.3^\circ\text{C}$). Data from birds with T_b above this threshold were discarded. M_b measured before and after trials were averaged, and these values were used for Msum analyses. Birds were brought back to their cage with food and water ad lib. until BMR measurement.

We measured the BMR of the four birds simultaneously from 1900 to 0600 hours. Measurements were done at 30°C (within the thermoneutral zone for this species; Chaplin 1976), using a constant flow of CO_2 -free dry air (average = 470 mL min^{-1}). As for Msum, birds were weighed before and after measurements, and average M_b were used in BMR analyses.

Oxygen analyzers were adjusted each day to 20.95% O_2 using CO_2 -free dry air. Mass flow valves (Side-Trak model 840, Sierra Instruments, Monterey, CA) were calibrated for air and helox using a bubble-O-meter (accurate within the tolerance $\pm 1\%$ 500-mL scale; Dublin, OH) once per winter. Metabolic rate calculations were done with ExpeData software (ver. 1.2.6; Sable Systems). Using a 20-s sampling interval for BMR and a 5-s interval for Msum, BMR and Msum calculations were based, respectively, on the lowest and highest averaged 10 min of oxygen consumption per measurement sequence, according to Lighton's equation [10.1] (Lighton 2008). We applied the instantaneous measurement technique (Bartholomew et al. 1981) for Msum calculations and a steady state approach for BMR. Duration of BMR trials (around 11 h) insured that birds were postabsorptive at time of BMR measurement. Since birds use lipids as fuel during fasting and for shivering (Swanson 2010), we estimated energy consumption using a constant equivalent of $19.8 \text{ kJ L}^{-1} \text{ O}_2$ and converted to watts (Gessaman and Nagy 1988). After BMR measurements, birds were put back in their cage with access to food and water until release on their capture site around 2 h later. In total, 180 Msum and 221 BMR were recorded for 101 and 114 individuals, respectively.

Capture-Mark-Recapture (CMR) Method

Each bird was marked at capture and released in the population after metabolic measurements. Besides capture sessions, to maximize our probability of resighting marked individuals, we also carried out an average of 1.9 (range = 1–6) observation sessions of 1 h per month on each site over the whole period of the study. We used both capture and observation from a distance as encounter occasions to calculate the return rate of birds, which depends on their probability of (1) surviving and coming back to the sampling site (Φ , the apparent survival probability) and (2) being encountered (p , the encounter probability). Using this protocol, birds from both cohorts were caught and resighted during the winter of their first capture (encounter occasions per bird within the first winter: cohort 1 = 2.5 ± 0.1 ; cohort 2 = 2.0 ± 0.2) and, for cohort 1, also during the fol-

lowing two winters (total encounter occasions per bird of cohort 1 = 4.1 ± 0.2). CMR protocol allowed us to record the encounter history of each bird. For example, an encounter history of 101 meant that a bird had been caught at the first encounter occasion, missed during the second occasion, and resighted during the third occasion. To calculate short-term survival (i.e., within-winter survival), we used CMR data collected for both cohorts during the winter of their first capture (i.e., winter 2009–2010 for cohort 1 and winter 2010–2011 for cohort 2), while we calculated long-term survival (i.e., among-year survival) using CMR data of cohort 1 collected from September 2009 to December 2011.

Statistical Analysis

Data Preparation. Total body mass and size-independent body mass (M_s) are expected to be related to individual condition (Norte et al. 2009). However, because they were highly correlated ($r = 0.80$), we could not include both variables in the analyses and therefore used only M_s as a measure of condition. Besides a seasonal increase in lean mass and fat reserves (Petit et al. 2013, 2014), wintering black-capped chickadees also follow a daily fattening cycle during which they store fat from sunrise to sunset, which is depleted during the night (Lehikoinen 1987; Mandin and Vézina 2012). Consequently, M_s in our birds depended on the time they were caught both during the winter and during the day. Hence, to calculate M_s , we first performed a principal component analysis on morphological data (length of head plus beak, wing, and tarsus; Rising and Somers 1989) to obtain an index (PC1) of structural body size (hereafter size). Then, we added size ($F_{1,595} = 333.7, P < 0.0001$) in a general linear model testing for the effects of date ($F_{1,595} = 14.5, P < 0.001$) and the variable relative time of capture (time since sunrise/day length; hereafter time of capture; $F_{1,595} = 79.5, P < 0.0001$) on M_b and used the residuals as our values of M_s .

BMR was dependent on M_b ($F_{1,222} = 46.0, P < 0.0001$) but not on date ($P = 0.3$), while Msum was influenced by both M_b ($F_{1,178} = 31.7, P < 0.0001$) and date ($F_{1,178} = 13.9, P < 0.001$). We therefore conducted two sets of survival analyses, one including raw BMR and Msum and the other including residual BMR and residual Msum, controlling for the effect of M_b and date.

We used raw Hct values in survival analyses because Hct was not related to date ($P = 0.7$), time of capture ($P = 0.5$), M_b ($P = 0.3$), or size ($P = 0.6$). When a bird was measured several times within a winter (for within-winter analyses) or in more than one winter (for the among-year analyses), we calculated the mean of each physiological parameter for a given bird and used these means in the survival analyses.

Our analyses were therefore conducted using both raw and residuals of BMR and Msum. However, when one of the residual parameters was found to significantly affect apparent survival, we reported corresponding back-calculated values (hereafter corrected BMR and Msum) in the text and figures to allow for comparison with other studies. These analyses were performed with R (ver. 3.0.3; R Development Core Team 2014).

Selection of the Basic Model. M_s , Hct, BMR, and Msum were available for 81 individuals for the within-winter survival analysis and for 56 individuals for the among-year analysis; we therefore restricted our data sets to these birds for further analyses. Survival analyses were performed using the software MARK (ver. 7.2; White and Burnham 1999). To analyze within-winter survival ($n = 81$), we used data recorded during the first winter for cohort 1 and data from the second winter for cohort 2. For both winters, we grouped encounter occasions in three periods (period 1 = September–November; period 2 = December–January; period 3 = February–March; see table S1; tables S1, S2 available online). Cormack-Jolly-Seber (CJS) models are based on live captures and releases of marked individuals into the population. We therefore analyzed the effects of cohort (1 and 2), age at first capture (juvenile and adult), and period on the return rate by testing for an effect of group (group 1 = cohort 1/adult; group 2 = cohort 1/juvenile; group 3 = cohort 2/adult; group 4 = cohort 2/juvenile) and period on both survival and encounter probabilities (return rate = $\Phi(g \times t)p(g \times t)$).

For among-year survival analyses ($n = 56$), we used data from only cohort 1. We grouped encounter data in seven periods (period 1 = September–November 2009; period 2 = December 2009–January 2010; period 3 = February–March 2010; period 4 = September–November 2010; period 5 = December 2010–January 2011; period 6 = February–March 2011; period 7 = November–December 2011; see table S2). We analyzed the relationship between age at first capture, periods, and return rate by testing the effect of group (group 1 = adult; group 2 = juvenile) and period on both survival and encounter probabilities (return rate = $\Phi(g \times t)p(g \times t)$).

We first tested whether our data fitted the full time-dependent CJS model (return rate = $\Phi(g \times t)p(g \times t)$), using the median \hat{c} estimator provided by MARK to estimate the overdispersion of our data. Because the median overdispersion factor (\hat{c}) was always inferior to 3, we used CJS models for further analyses. However, when median \hat{c} was superior to 1, we multiplied the variance-covariance matrix by median \hat{c} to control for the overdispersion of our data.

For both within-winter and among-year survival analyses, the model with the lowest second-order Akaike information criterion (corrected AIC [AICc] or modified AICc [QAICc] when the matrix was multiplied by median \hat{c}) was selected as the basic model. Then, we used the likelihood ratio test provided by MARK to compare models and analyze the significance of the factors group and period. In the within-winter

analyses, the effects of group and period were not significant (see “Results”); we therefore used the null model (return rate = $\Phi(.)p(.)$) as the basic model for these analyses. In the among-year analyses, the effect of period was significant on the encounter probability (see “Results”); we therefore used the model return rate = $\Phi(.)p(t)$ as the basic model for the among-year analyses.

Effect of Physiological Parameters on Survival. We analyzed the effect of physiological parameters on both within-winter and among-year survival by including average M_s , Hct, BMR, and Msum (raw and residuals considered in separate sets of analyses) as covariates in the basic models (full model within winter: $\Phi(M_s + M_s^2 + \text{Hct} + \text{Hct}^2 + \text{BMR} + \text{BMR}^2 + \text{Msum} + \text{Msum}^2)p(.)$; among years: $\Phi(M_s + M_s^2 + \text{Hct} + \text{Hct}^2 + \text{BMR} + \text{BMR}^2 + \text{Msum} + \text{Msum}^2)p(t)$), and we selected the model with the lowest AICc (or QAICc) as the best model. Then, we used likelihood ratio tests to determine the significance of the covariates. When the software MARK is used to analyze the effect of a continuous variable on survival, it outputs survival probabilities according to predicted values based on the entered data. These new predicted values are not statistically controlling for additional variables and remain in the same units as the original variable included in the model. This means that when using residual BMR and residual Msum as continuous variables in our analyses, MARK provided survival probabilities for newly generated residuals of BMR and Msum. Because residuals are inconvenient for comparing results between studies, we back-calculated BMR and Msum from the data provided by MARK. To do so, we used our complete data set (BMR: $n = 221$; Msum: $n = 180$) and ran regressions between BMR and Msum and their residuals controlling for M_b and date. Then, we used the regression equations to back-calculate BMR and Msum values (hereafter corrected BMR and Msum) from residual BMR and Msum (controlling for M_b and date) that were produced by MARK.

Results

Physiological Adjustments

Within winter (cohort 1: September 2009–March 2010; cohort 2: September 2010–March 2011), body mass ($F_{2,281} = 11.2$, $P < 0.0001$), Hct ($F_{2,196} = 21.2$, $P < 0.0001$), mass-independent BMR ($F_{2,152} = 5.8$, $P < 0.01$), and mass-independent Msum ($F_{2,120} = 36.5$, $P < 0.0001$) depended on period (table 1). Body mass increased by 3.0% (Tukey’s test: $P < 0.0001$) between pe-

Table 1: Physiological adjustments within winter for both cohorts

	P1	P2	P3
Body mass (g)	11.30 ± .07	11.64 ± .06	11.56 ± .05
Hct	.484 ± .003	.516 ± .003	.509 ± .003
Mass-independent BMR (W)	.246 ± .004	.266 ± .004	.266 ± .003
Mass-independent Msum (W)	1.240 ± .026	1.546 ± .030	1.672 ± .029

Note. Period 1 (P1) = September–November; P2 = December–January; P3 = February–March. Hct = hematocrit; BMR = basal metabolic rate; Msum = summit metabolic rate.

Table 2: Physiological adjustments among years for cohort 1

	P1 ^a	P2	P3	P4	P5	P6	P7 ^b
Body mass (g)	11.49 ± .09	11.77 ± .08	11.61 ± .06	11.23 ± .15	11.70 ± .16	11.52 ± .12	
Hct	.487 ± .005	.522 ± .003	.506 ± .004	.466 ± .007	.513 ± .008	.521 ± .008	
Mass-independent BMR (W)		.271 ± .005	.265 ± .004	.248 ± .006	.268 ± .004	.259 ± .006	
Mass-independent Msum (W)		1.610 ± .050	1.715 ± .042	1.321 ± .027	1.533 ± .047	1.589 ± .025	

Note. Period 1 (P1) = September–November 2009; P2 = December 2009–January 2010; P3 = February–March 2010; P4 = September–November 2010; P5 = December 2010–January 2011; P6 = February–March 2011; P7 = November–December 2011. Hct = hematocrit; BMR = basal metabolic rate; Msum = summit metabolic rate.

^aMetabolic performance was not measured during P1.

^bDuring P7, birds were resighted by observation but not captured.

riod 1 (September–November) and period 2 (December–January) and stayed constant until period 3 (February–March; Tukey’s test: $P = 0.6$). Hct also increased by 6.5% between September–November and December–January and stayed constant until February–March (Tukey’s test: $P = 0.4$). Chickadees improved their mass-independent Msum during the whole winter, with an increased by 34.8% from September–November to February–March (Tukey’s test: $P < 0.001$). Concerning BMR adjustment within winter, the observed increase in mass-independent BMR of 7.9% between September–November and December–January was not significant (Tukey’s test: $P = 0.15$).

Among years (September 2009–March 2011), body mass ($F_{5,269} = 6.7, P < 0.0001$), Hct ($F_{5,94} = 14.2, P < 0.0001$), and mass-independent Msum ($F_{4,92} = 8.5, P < 0.0001$) but not mass-independent BMR ($F_{4,134} = 2.1, P = 0.08$) were influenced by period (table 2). During both years, cohort 1 expressed a higher body mass at midwinter than at the beginning of win-

ter (year 1: +2.5%; Tukey’s test: $P < 0.0001$; year 2: +4.1%; Tukey’s test: $P = 0.07$). Hct followed the same pattern with higher values at midwinter than at the beginning of winter during both years (year 1: +7.2%; Tukey’s test: $P < 0.001$; year 2: +9.9%; Tukey’s test: $P < 0.001$). Technical difficulties prevented us from measuring metabolic performance during the first period (September–November 2009). However, although BMR was not significantly different over periods, we noticed that chickadees expressed their maximal BMR during midwinter in both years and that Msum increased during winter to reach its highest values at the end of winter (table 2).

Within-Winter Survival

Within-winter return rate did not depend on group ($\chi^2 = 5.1, P = 0.2$) or period ($\chi^2 = 0.5, P = 0.5$). On the basis of the AICc, the best model explaining our data was the null model

Table 3: Model selection testing for the effect of period and group (i.e., cohort and age) on the return rate of both cohorts during winter

No.	Model	AICc	Δ AICc	W_{AICc}	Likelihood	Parameters	Deviance
1	$\Phi(.)p(.)$	87.1	.0	.3	1.00	2	14.9
2	$\Phi(g)p(.)$	88.7	1.6	.1	.45	5	9.8
3	$\Phi(.)p(t)$	88.8	1.7	.1	.43	3	14.4
4	$\Phi(t)p(.)$	88.8	1.7	.1	.43	3	14.4
5	$\Phi(t)p(t)$	88.8	1.7	.1	.43	3	14.4
6	$\Phi(g)p(g)$	89.9	2.8	.1	.24	7	6.2
7	$\Phi(g)p(t)$	90.8	3.7	.0	.16	6	9.5
8	$\Phi(.)p(g)$	92.0	4.9	.0	.09	5	13.1
9	$\Phi(t)p(g)$	93.5	6.4	.0	.04	6	12.3
10	$\Phi(g \times t)p(t)$	94.9	7.8	.0	.02	8	8.6
11	$\Phi(t)p(g \times t)$	95.1	8.0	.0	.02	8	8.8
12	$\Phi(.)p(g \times t)$	95.3	8.2	.0	.02	8	9.0
13	$\Phi(g \times t)p(.)$	95.3	8.2	.0	.02	8	9.1
14	$\Phi(g \times t)p(g \times t)$	96.3	9.2	.0	.01	10	4.8
15	$\Phi(g)p(g \times t)$	96.5	9.4	.0	.01	10	5.0
16	$\Phi(g \times t)p(g)$	97.6	10.5	.0	.01	10	6.1

Note. Mean $\hat{c} = 1.0$. t = period with three levels: 1 = September–November; 2 = December–January; 3 = February–March. g = group with four levels: 1 = cohort 1/adult; 2 = cohort 1/juvenile; 3 = cohort 2/adult; 4 = cohort 2/juvenile. AICc = corrected Akaike information criterion; W_{AICc} = weight of the model.

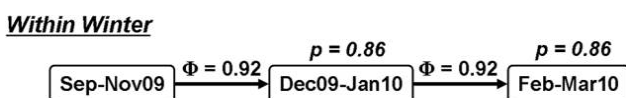


Figure 1. Within-winter survival and encounter probabilities. Diagram represents both the apparent survival (Φ) and the encounter probabilities (p) within winter. Apparent survival and encounter probability are constant.

$\Phi(\cdot)p(\cdot)$ (table 3). Hence, for both cohorts combined together, the apparent survival probability as well as the encounter probability were high and constant throughout winter and age ($\Phi = 0.92 \pm 0.05$, $p = 0.86 \pm 0.06$; fig. 1).

Once we added covariates to the null model, we observed that the within-winter return rate was best explained by a model where the survival probability was dependent on Hct and residuals of Msum ($\Phi(\text{Hct} + \text{resMsum})p(\cdot)$; table 4). Analyses of the covariate effects showed that winter survival varied with residual Msum and Hct. However, only residual Msum is significant ($\Phi(\cdot)p(\cdot)$ vs. $\Phi(\text{resMsum})p(\cdot)$: $\chi^2 = 10.7$, $P < 0.01$; $\Phi(\cdot)p(\cdot)$ vs. $\Phi(\text{Hct})p(\cdot)$: $\chi^2 = 1.7$, $P = 0.2$). Within-winter survival was not related to M_s ($\Phi(\cdot)p(\cdot)$ vs. $\Phi(M_s)p(\cdot)$: $\chi^2 = 0.03$, $P = 0.96$) or residual BMR ($\Phi(\cdot)p(\cdot)$ vs. $\Phi(\text{resBMR})p(\cdot)$: $\chi^2 = 0.1$, $P = 0.8$).

The relationship between Msum and residual Msum controlling for M_b and date was linear and strong ($r = 0.89$, $n = 180$, $P < 0.0001$) allowing us to use the regression equation (Msum = $1.535 + \text{residual Msum}$) to calculate corrected Msum from

residual Msum. The relationship between winter survival and corrected Msum followed a nonlinear curve (fig. 2a). Below a corrected Msum of 1.17 W, winter survival probability was $< 10\%$; between 1.20 and 1.32 W, survival probability increased linearly, reaching 50% at 1.26 W. When birds expressed an average corrected Msum above 1.35 W, winter survival probability was $> 90\%$, and individuals with a corrected Msum superior to 1.46 W were expected to have a 100% chance of survival.

Analyses with raw BMR and raw Msum showed that the within-winter return rate was best explained by a model where the survival probability was dependent on BMR and Msum ($\Phi(\text{BMR} + \text{Msum})p(\cdot)$; table 5). Analyses of the covariate effects revealed that within-winter survival varied with Msum and BMR. However, only Msum is significant ($\Phi(\cdot)p(\cdot)$ vs. $\Phi(\text{Msum})p(\cdot)$: $\chi^2 = 13.2$, $P < 0.001$; $\Phi(\cdot)p(\cdot)$ vs. $\Phi(\text{BMR})p(\cdot)$: $\chi^2 = 0.3$, $P = 0.6$). Within-winter survival was not related to M_s ($\Phi(\cdot)p(\cdot)$ vs. $\Phi(M_s)p(\cdot)$: $\chi^2 = 0.03$, $P = 0.96$) or Hct ($\Phi(\cdot)p(\cdot)$ vs. $\Phi(\text{Hct})p(\cdot)$: $\chi^2 = 1.7$, $P = 0.2$) in this case. The relationship between winter survival and raw Msum followed a sigmoid curve (fig. 2b). Below an Msum of 1.35 W, within-winter survival probability was null, while above 1.35 W, within-winter survival probability was 100%.

Among-Year Survival

Among years, the return rate did not depend on group ($\chi^2 = 0.9$, $P = 0.3$) but was influenced by period ($\chi^2 = 12.8$, $P <$

Table 4: Model selection testing for the effect of mean size-independent body mass (M_s), hematocrit (Hct), residual basal metabolic rate (resBMR), and residual summit metabolic rate (resMsum) on the return rate of both cohorts during winter

No.	Model	AICc	ΔAICc	W_{AICc}	Likelihood	Parameters	Deviance
1	$\Phi(\text{Hct} + \text{resMsum})p(\cdot)$	76.0	.0	.3	1.00	4	67.4
2	$\Phi(\text{Hct} + \text{resBMR} + \text{resMsum})p(\cdot)$	76.6	.6	.2	.73	5	65.7
3	$\Phi(M_s + M_s^2 + \text{Hct} + \text{Hct}^2 + \text{resBMR} + \text{resBMR}^2 + \text{resMsum} + \text{resMsum}^2)p(\cdot)$	78.2	2.2	.1	.33	10	54.7
4	$\Phi(M_s + \text{Hct} + \text{resMsum})p(\cdot)$	78.2	2.3	.1	.32	5	67.4
5	$\Phi(M_s + \text{Hct} + \text{resBMR} + \text{resMsum})p(\cdot)$	78.7	2.7	.1	.26	6	65.4
6	$\Phi(\text{resMsum})p(\cdot)$	79.1	3.1	.1	.21	3	72.7
7	$\Phi(\text{resBMR} + \text{resMsum})p(\cdot)$	80.3	4.4	.0	.11	4	71.8
8	$\Phi(M_s + M_s^2)p(\cdot)$	80.7	4.7	.0	.09	4	72.1
9	$\Phi(M_s + \text{resMsum})p(\cdot)$	80.7	4.8	.0	.09	4	72.2
10	$\Phi(M_s + \text{resBMR} + \text{resMsum})p(\cdot)$	81.0	5.1	.0	.08	5	70.2
11	$\Phi(\text{resMsum} + \text{resMsum}^2)p(\cdot)$	81.1	5.2	.0	.08	4	72.6
12	$\Phi(\text{Hct} + \text{Hct}^2)p(\cdot)$	87.5	11.6	.0	.00	4	78.9
13	$\Phi(\cdot)p(\cdot)$	87.5	11.6	.0	.00	2	83.4
14	$\Phi(\text{Hct})p(\cdot)$	88.0	12.0	.0	.00	3	81.6
15	$\Phi(\text{resBMR})p(\cdot)$	89.7	13.7	.0	.00	3	83.3
16	$\Phi(M_s)p(\cdot)$	89.7	13.8	.0	.00	3	83.4
17	$\Phi(M_s + \text{Hct})p(\cdot)$	90.0	14.0	.0	.00	4	81.4
18	$\Phi(\text{Hct} + \text{resBMR})p(\cdot)$	90.2	14.2	.0	.00	4	81.6
19	$\Phi(M_s + \text{resBMR})p(\cdot)$	91.9	15.9	.0	.00	4	83.3
20	$\Phi(\text{resBMR} + \text{resBMR}^2)p(\cdot)$	91.9	15.9	.0	.00	4	83.3
21	$\Phi(M_s + \text{Hct} + \text{resBMR})p(\cdot)$	92.2	16.2	.0	.00	5	81.3

Note. Mean $\hat{c} = 1.0$. AICc = corrected Akaike information criterion; W_{AICc} = weight of the model.

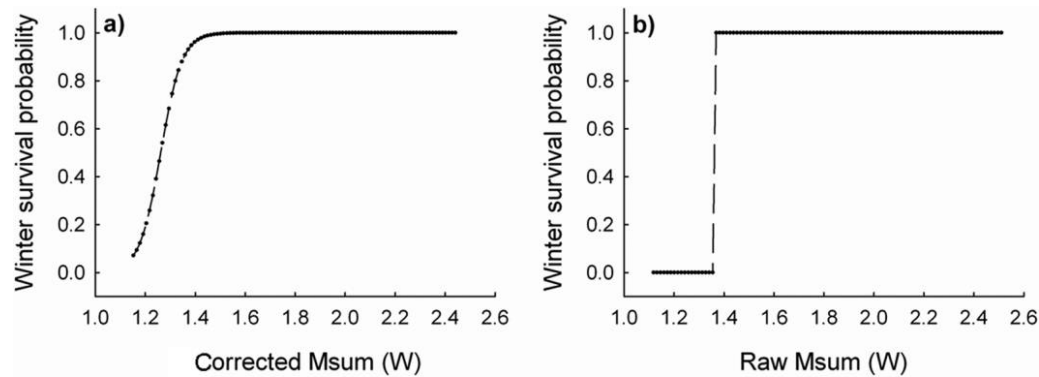


Figure 2. Effect of thermogenic capacity on within-winter survival. Relationship between winter apparent survival and winter corrected summit metabolic rate (Msum), controlling for body mass and date of measure, with survival controlled for the effect of hematocrit (a), and winter raw Msum, with survival controlled for the effect of basal metabolic rate (b).

0.05). On the basis of the QAICc, the best model explaining our data was the model $\Phi(\cdot)p(t)$ (table 6). Hence, the apparent survival probability was high and constant among periods and ages ($\Phi = 0.96 \pm 0.02$), but the encounter probability varied over time. Specifically, encounter probability was lower in the beginning of winter than during the rest of the season (fig. 3).

With the covariates included in the model $\Phi(\cdot)p(t)$, among-year return rate was best explained by a model including

residuals of Msum and size-independent body mass ($\Phi(M_s + \text{resMsum})p(t)$; table 7). However, the effects of residual Msum and M_s alone or combined were not significant ($\Phi(\cdot)p(t)$ vs. $\Phi(\text{resMsum})p(t)$: $\chi^2 = 2.7$, $P = 0.1$; $\Phi(\cdot)p(t)$ vs. $\Phi(M_s)p(t)$: $\chi^2 = 2.8$, $P = 0.1$; $\Phi(\cdot)p(t)$ vs. $\Phi(M_s + \text{resMsum})p(t)$: $\chi^2 = 5.8$, $P = 0.06$). Among-year return rate was not dependent on Hct ($\Phi(\cdot)p(t)$ vs. $\Phi(\text{Hct})p(t)$: $\chi^2 = 0.0$, $P = 1.0$) or on residuals of BMR ($\Phi(\cdot)p(t)$ vs. $\Phi(\text{BMR})p(t)$: $\chi^2 = 0.2$, $P = 0.6$) either.

Table 5: Model selection testing for the effect of mean size-independent body mass (M_s), hematocrit (Hct), basal metabolic rate (BMR), and summit metabolic rate (Msum) on the return rate of both cohorts during winter

No.	Model	AICc	ΔAICc	W_{AICc}	Likelihood	Parameters	Deviance
1	$\Phi(\text{BMR} + \text{Msum})p(\cdot)$	63.6	.0	.49	1.00	4	55.1
2	$\Phi(\text{Hct} + \text{BMR} + \text{Msum})p(\cdot)$	65.9	2.3	.16	.32	5	55.1
3	$\Phi(M_s + \text{BMR} + \text{Msum})p(\cdot)$	65.9	2.3	.16	.32	5	55.1
4	$\Phi(M_s + \text{Hct} + \text{BMR} + \text{Msum})p(\cdot)$	65.9	2.3	.16	.32	5	55.1
5	$\Phi(M_s + M_s^2 + \text{Hct} + \text{Hct}^2 + \text{BMR} + \text{BMR}^2 + \text{Msum} + \text{Msum}^2)p(\cdot)$	68.9	5.2	.04	.07	7	53.2
6	$\Phi(\text{Hct} + \text{Msum})p(\cdot)$	76.2	12.6	.00	.00	4	67.6
7	$\Phi(\text{Msum})p(\cdot)$	76.5	12.9	.00	.00	3	70.2
8	$\Phi(M_s + \text{Hct} + \text{Msum})p(\cdot)$	78.5	14.9	.00	.00	5	67.6
9	$\Phi(M_s + \text{Msum})p(\cdot)$	78.7	15.1	.00	.00	4	70.2
10	$\Phi(\text{Msum} + \text{Msum}^2)p(\cdot)$	78.7	15.1	.00	.00	4	70.2
11	$\Phi(M_s + M_s^2)p(\cdot)$	80.7	17.1	.00	.00	4	72.1
12	$\Phi(\text{Hct} + \text{Hct}^2)p(\cdot)$	87.5	23.9	.00	.00	4	79.0
13	$\Phi(\cdot)p(\cdot)$	87.5	23.9	.00	.00	2	83.4
14	$\Phi(\text{Hct})p(\cdot)$	88.0	24.3	.00	.00	3	81.6
15	$\Phi(\text{BMR})p(\cdot)$	89.4	25.8	.00	.00	3	83.1
16	$\Phi(M_s)p(\cdot)$	89.7	26.1	.00	.00	3	83.4
17	$\Phi(M_s + \text{Hct})p(\cdot)$	90.0	26.3	.00	.00	4	81.4
18	$\Phi(\text{Hct} + \text{BMR})p(\cdot)$	90.1	26.5	.00	.00	4	81.6
19	$\Phi(\text{BMR} + \text{BMR}^2)p(\cdot)$	91.4	27.8	.00	.00	4	82.8
20	$\Phi(M_s + \text{BMR})p(\cdot)$	91.6	28.0	.00	.00	4	83.1
21	$\Phi(M_s + \text{Hct} + \text{BMR})p(\cdot)$	92.2	28.6	.00	.00	5	81.3

Note. Mean $\hat{c} = 1.0$. AICc = corrected Akaike information criterion; W_{AICc} = weight of the model.

Table 6: Model selection testing for the effect of period and age on the return rate of cohort 1 between years

No.	Model	QAICc	Δ QAICc	W_{QAICc}	Likelihood	Parameters	QDeviance
1	$\Phi(\cdot)p(t)$	223.2	.0	.4	1.00	7	77.4
2	$\Phi(g)p(t)$	224.7	1.4	.2	.49	8	76.7
3	$\Phi(\cdot)p(\cdot)$	225.5	2.2	.1	.33	2	90.2
4	$\Phi(t)p(t)$	225.7	2.5	.1	.29	11	71.0
5	$\Phi(g)p(\cdot)$	226.6	3.4	.1	.19	3	89.3
6	$\Phi(\cdot)p(g)$	227.4	4.2	.1	.12	3	90.1
7	$\Phi(g)p(g)$	228.7	5.5	.0	.07	4	89.3
8	$\Phi(t)p(\cdot)$	231.3	8.1	.0	.02	7	85.5
9	$\Phi(t)p(g)$	233.4	10.1	.0	.01	8	85.4
10	$\Phi(\cdot)p(g \times t)$	233.8	10.6	.0	.01	13	74.5
11	$\Phi(g)p(g \times t)$	235.9	12.7	.0	.00	14	74.3
12	$\Phi(t)p(g \times t)$	236.0	12.7	.0	.00	17	67.2
13	$\Phi(g \times t)p(t)$	237.7	14.5	.0	.00	17	68.9
14	$\Phi(g \times t)p(\cdot)$	242.0	18.8	.0	.00	13	82.7
15	$\Phi(g \times t)p(g)$	244.3	21.1	.0	.00	14	82.7
16	$\Phi(g \times t)p(g \times t)$	247.3	24.1	.0	.00	22	66.0

Note. Mean $\hat{c} = 1.557$. t = period with seven levels: 1 = September–November 2009; 2 = December 2009–January 2010; 3 = February–March 2010; 4 = September–November 2010; 5 = December 2010–January 2011; 6 = February–March 2011; 7 = November–December 2011. g = group with two levels: 1 = adult; 2 = juvenile. QAICc = modified corrected Akaike information criterion; W_{QAICc} = weight of the model; QDeviance = modified deviance.

Analyses with raw BMR and raw Msum gave the same results (not shown). Therefore, long-term survival was not dependent on any of the measured physiological parameter.

Discussion

In this study, we investigated the effect of winter metabolism on survival of free-living black-capped chickadees. We expected a positive and nonlinear effect of winter physiological condition on both within-winter and among-year survival. Our results showed that within-winter survival was indeed positively and nonlinearly related to maximal thermogenic capacity. However, although size-independent body mass and residual Msum were highlighted as potentially important, survival among years

was not dependent on any of the measured physiological parameter. This study is therefore the first to show the benefit of increasing winter thermogenic capacity for survival—a proxy of fitness—in free-living birds.

High Winter Survival in Black-Capped Chickadees

Apparent survival probability was high (0.92) within winter and remained constant throughout the season, despite the seasonal peak of cold occurring in midwinter (Petit et al. 2013). This finding is consistent with observations in chickadees made by others (Desrochers et al. 1988; Egan and Brittingham 1994), including in food-supplemented populations (Egan and Brittingham 1994). Long-term apparent survival was also high (0.96)

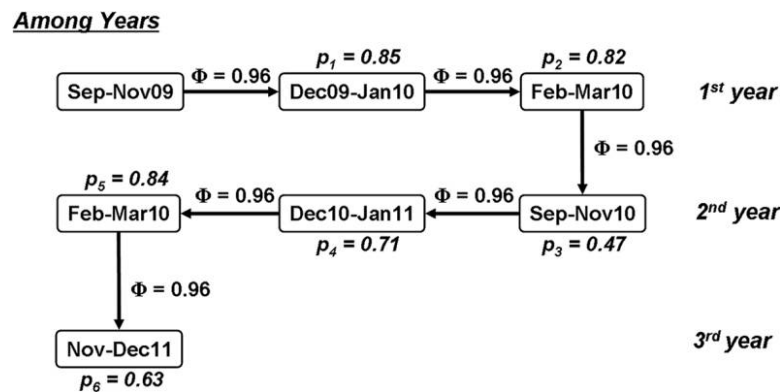


Figure 3. Between-winter survival and encounter probabilities. Diagram represents both the apparent survival (Φ) and the encounter probabilities (p) among years. Apparent survival was constant, while encounter probabilities decreased between the end of a winter and the beginning of the next one.

Table 7: Model selection testing for the effect of mean size-independent body mass (M_s), hematocrit (Hct), residual basal metabolic rate (resBMR), and residual summit metabolic rate (resMsum) on the return rate of cohort 1 among years

No.	Model	QAICc	Δ QAICc	W_{QAICc}	Likelihood	Parameters	QDeviance
1	$\Phi(M_s + \text{resMsum})p(t)$	227.0	.0	.2	1.00	9	208.0
2	$\Phi(M_s)p(t)$	227.8	.8	.1	.68	8	211.0
3	$\Phi(\text{resMsum})p(t)$	227.9	.9	.1	.63	8	211.1
4	$\Phi(.)p(t)$	228.4	1.4	.1	.49	7	213.8
5	$\Phi(M_s + \text{resBMR} + \text{resMsum})p(t)$	229.2	2.2	.1	.33	10	208.0
6	$\Phi(M_s + \text{Hct} + \text{resMsum})p(t)$	229.2	2.2	.1	.33	10	208.0
7	$\Phi(M_s + \text{resBMR})p(t)$	229.6	2.6	.1	.27	9	210.6
8	$\Phi(M_s + M_s^2)p(t)$	229.9	2.9	.0	.24	9	210.9
9	$\Phi(\text{resMsum} + \text{resMsum}^2)p(t)$	229.9	2.9	.0	.23	9	210.9
10	$\Phi(M_s + \text{Hct})p(t)$	230.0	3.0	.0	.23	9	211.0
11	$\Phi(\text{Hct} + \text{resMsum})p(t)$	230.0	3.0	.0	.22	9	211.0
12	$\Phi(\text{resBMR} + \text{resMsum})p(t)$	230.1	3.1	.0	.21	9	211.1
13	$\Phi(\text{resBMR})p(t)$	230.4	3.4	.0	.18	8	213.6
14	$\Phi(\text{Hct})p(t)$	230.6	3.6	.0	.16	8	213.8
15	$\Phi(M_s + \text{Hct} + \text{resBMR} + \text{resMsum})p(t)$	231.5	4.5	.0	.11	11	208.0
16	$\Phi(M_s + \text{Hct} + \text{resBMR})p(t)$	231.8	4.8	.0	.09	10	210.6
17	$\Phi(.)p(.)$	231.9	4.9	.0	.09	2	227.8
18	$\Phi(\text{Hct} + \text{resBMR} + \text{resMsum})p(t)$	232.2	5.3	.0	.07	10	211.0
19	$\Phi(\text{resBMR} + \text{resBMR}^2)p(t)$	232.4	5.4	.0	.07	9	213.4
20	$\Phi(\text{Hct} + \text{Hct}^2)p(t)$	232.5	5.5	.0	.06	9	213.5
21	$\Phi(\text{Hct} + \text{resBMR})p(t)$	232.6	5.6	.0	.06	9	213.6
22	$\Phi(M_s + M_s^2 + \text{Hct} + \text{Hct}^2 + \text{resBMR} + \text{resBMR}^2 + \text{resMsum} + \text{resMsum}^2)p(t)$	239.6	12.6	.0	.00	15	206.9

Note. Mean $\hat{c} = 1.557$. t = period with seven levels: 1 = September–November 2009; 2 = December 2009–January 2010; 3 = February–March 2010; 4 = September–November 2010; 5 = December 2010–January 2011; 6 = February–March 2011; 7 = November–December 2011. QAICc = modified corrected Akaike information criterion; W_{QAICc} = weight of the model; QDeviance = modified deviance.

and constant among years. Loery et al. (1997) and Schubert et al. (2008) suggested that differences in survival between years result from environmental variability, such as change in food availability or in habitat. Given the lack of year effect on survival, our results therefore imply that our population of black-capped chickadees faced a relatively stable environment during the 3 yr of the study.

Survival—whether considered within or among winters—was not related to age. Since the highest rates of mortality in juvenile birds occurs during the nestling and fledgling stages (Perrins 1965; Smith 1967; Sullivan 1989), this finding suggests that the juvenile chickadees that were captured during winter had passed this critical point and were equally likely to survive as the adults.

Influence of Metabolic Performance on Survival

Several studies made the assumption that by increasing metabolic performance, wintering birds improve their chances of survival (Swanson and Olmstead 1999; Sears et al. 2006; Nzama et al. 2010; Petit et al. 2013). We therefore expected to find positive but nonlinear relationships between survival and winter levels of both BMR and Msum in black-capped chickadees. Fur-

thermore, since it appears to support thermogenic capacity (Petit and Vézina 2014a), we also expected a positive relationship between survival and Hct. Our results only partially supported these predictions. They showed that BMR and Hct alone did not affect survival probability but that birds expressing a high Msum were more likely to survive through a given winter and even more so if they also had a high Hct. Winter acclimatization is associated with the growth of several internal organs in small birds (Liu and Li 2006; Zheng et al. 2008; Liknes and Swanson 2011b; Petit et al. 2014). It is thought that this organ development supports a seasonal increase in foraging as well as general thermoregulation needs and that this in turn leads to an increase in basal metabolism (Cooper and Swanson 1994; Petit et al. 2013). Because we found no influence of winter BMR alone on survival, it appears that this enhanced support capacity and the associated benefit for heat production are not sufficient to improve chances of winter survival. Similarly, although midrange Hct levels seem optimal to support high winter Msum (around 0.53, parabolic relationship; see Petit and Vézina 2014a), this parameter is nevertheless quite variable among chickadees (Petit and Vézina 2014a). Winter Hct may therefore have to reach extreme values (e.g., severe anemia) before an effect of this variable alone can be observed on survival.

Birds Improve Their Thermogenic Capacity Ahead of Time to Increase Their Chances of Winter Survival

Within-winter survival was positively related to maximal thermogenic capacity. Birds measured during winter that had an average corrected Msum below 1.26 W (representing 5% of our population) had a <50% chance of survival, while birds with an average corrected Msum above 1.35 W (representing 95% of our population) had at least a 90% chance of surviving through the winter (fig. 2a). Using raw Msum rather than residual Msum in our analyses resulted in the same observation, although the relationship between winter survival and maximal thermogenic capacity was less nuanced. In this case, the cutoff value for survival was 1.35 W. Below this point, birds had no chance of survival (15% of our population), and above this point, birds were expected to survive the winter season (85% of the population; fig. 2b). In this study, chickadees increased their mass-corrected Msum within winter from 1.24 W (corresponding to a <50% chance of survival at best) in September–November to reach an average value of 1.55 W (corresponding to a 100% chance of survival) in December–January. Similarly, in previous studies on the same chickadee population (Petit et al. 2013, 2014), we found that summer (August) levels of raw Msum were on average 1.26 W (M. Petit and F. Vézina, unpublished data), a value that should confer to wintering individuals a <50% chance of survival at best (using data corrected for body mass and date of capture). We also showed that Msum in this species begins to increase before October (Petit et al. 2013) and perhaps even as early as the end of August (Petit and Vézina 2014b). Therefore, not only do black-capped chickadees apparently have to increase their thermogenic capacity well ahead of the peak of winter cold in order to maximize their winter survival, but also it seems that individuals that are either too slow or unable to adjust their phenotype from summer to winter have a <50% chance of surviving. Because temperature is the main driver of Msum variations in this and other species (Swanson and Olmstead 1999; Petit and Vézina 2014b; Swanson et al. 2014), it is likely that thermogenic capacity begins to increase as soon as the birds encounter the first cold nights of the early autumn (Petit et al. 2013). The actual level of heat loss required to trigger this upregulation remains, however, to be investigated. Our data therefore confirm for the first time in birds that increasing thermogenic capacity does improve winter survival in small-bodied species.

Why Maintain a Higher Msum than Needed for Survival?

We predicted that chickadees would express maximal survival probability at intermediate Msum levels. However, although the relationship between survival and thermogenic capacity was positive and nonlinear, apparent survival was not compromised when Msum reached its highest level. Indeed, our data (see tables 1, 2) suggest that winter Msum could be maintained at average levels well above 1.35 W (90% survival) or even above 1.46 W, the threshold value associated with 100% survival (fig. 2). For example, chickadees from the first cohort measured between February and March 2011 expressed an average level of

Msum of 1.59 W. That is 9 % higher than the heat production capacity seemingly guaranteeing maximal within-winter survival in our population. One can wonder then why would birds maintain a winter Msum as high as 1.59 W if it does not further improve chances of survival and thus fitness? Since upregulating muscle size for endurance exercise also leads to an increase in thermogenic capacity (Swanson 1995; Swanson and Dean 1999; Vézina et al. 2007), one hypothesis is that chickadees could maintain large flight muscles in the winter primarily for active foraging to maximize food intake at the coldest time of the year, while the increase in thermogenic performance would in fact be an added benefit. Comparing birds experimentally trained for active exercise and cold would be one way to test this hypothesis (Zhang et al. 2015).

High Winter Thermogenic Capacity Does Not Guarantee Long-Term Survival

Our results revealed that survival among years was not related to individual thermogenic capacity or any of our other physiological parameters. Given that birds adjust their phenotype ahead of the peak of cold, increasing Msum for the current season may improve an individual's immediate survival but seems not to guarantee survival among years. Although Msum can be repeatable across years (Cortés et al. 2015), it is nevertheless a highly flexible trait (Swanson 2010; Swanson and Vézina 2015) that, at the population scale, may differ between winters according to minimal ambient temperatures (Swanson and Olmstead 1999; Petit et al. 2013). Adjusting thermogenic capacity to a particular set of wintering conditions may therefore have little influence on long-term survival. Furthermore, other costly life-history stages—such as breeding or molt—also come with physiological constraints that may influence fitness (Jacobs and Wingfield 2000). Physiological constraints happening in the spring or summer may therefore affect individual condition and bear fitness consequences carrying over to the next winter (Harrison et al. 2011). This could prevent analyses from detecting effects of Msum—measured in a particular winter—on survival over several years.

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