

# Seasonal and temporal variation in scaled mass index of Black-capped Chickadees (*Poecile atricapillus*)

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## Abstract

Avian body mass reflects a trade-off between risk of starvation and predation, and may vary with ambient temperature, age, and time of day. Seasonal variability in body mass is a common occurrence in northern temperate regions, including adaptive fattening. Previous evidence suggests that seasonal variability is less pronounced in tree-feeding bird species, as their food sources during winter are less limited and variable compared to ground-foraging species. We determined fat scores of tree-feeding Black-capped Chickadees (*Poecile atricapillus*) captured year-round between 2004 and 2015 ( $n = 4248$ ) in southern Quebec, to test the relative strength of possible drivers of variability in chickadee body mass, including time, date, and year of capture, age, and temperature. First, we demonstrated that scaled mass index (SMI) was the body condition index, out of four possible indices tested, which most strongly correlated with fat scores measured in the field. We used SMI subsequently as our estimator of body condition to avoid observer effects associated with fat scores. Similar to other studies, time of capture significantly affected SMI, in which birds captured later were heavier, indicating that chickadees experience overnight weight loss and subsequent weight gain from foraging throughout the day. SMI was constant from April to November, then peaked in late winter, but was not influenced by daily temperature after accounting for month and year. SMI was not significantly affected by age. We concluded that adaptive fattening is an evolutionary response to risk of starvation in winter, rather than a proximal response to immediate ambient temperature.

Key words: Black-capped Chickadee; condition index; fat stores; scaled mass index; temperature; temporal; body mass

## Introduction

Body mass varies greatly within bird species, often representing variation in lipid mass, and reflecting costs and benefits to high lipid stores (Lindstedt and Boyce 1985; Cresswell 1998). Higher lipid deposits may increase survival during periods of food shortage because fatter individuals have more endogenous energy stores (Thomas 2000; Krams *et al.* 2009; Ratikainen and Wright 2013). In winter, these energy stores may also act as buffers against cold temperatures, as birds expend more energy for thermoregulation, as well as against short winter days when reduced foraging increases the risk of starvation (Brodin *et al.* 2017; Da Silva *et al.* 2017). However, costs to higher body mass due to higher lipid deposits may include reduced takeoff ability and more time spent foraging to maintain a high body mass, both of which can increase chances of predation (Gosler *et al.* 1995; MacLeod *et al.* 2005, 2008; Rogers 2015). Alternatively, variation in lipid deposits may be stress-induced rather than adaptive; a lower average body mass may reflect low food availability rather than a fitness optimum (Ketterson *et al.* 1991; Kitaysky *et al.* 1999).

In northern temperate regions with large climate ranges, the effect of seasonality on body mass is especially pronounced (Haftorn 1992; Rogers 1995; Cooper 2007; Polo *et al.* 2007). The concept of adaptive winter fattening, in which small birds residing in cold

habitats build up large fat reserves in response to low temperatures, has been widely studied (Haftorn 1989; Rogers 1995; Koenig *et al.* 2005; Merom *et al.* 2005) since its introduction by King and Farner in 1966. Weight gain in winter is caused by increased lipid deposits, which provide the metabolic fuel required to sustain an individual during winter fasts or food shortages (Lehikoinen 1987), as well as enlarged organs and muscles (Liu *et al.* 2008; Zheng *et al.* 2008, 2010; Liknes and Swanson 2011). Body mass tends to peak in mid-winter and decline thereafter (Haftorn 1989). Lower body mass in spring and summer may be attributed to physiological stress during the breeding season or adaptive reduction in wing-loading to ease the labour of feeding nestlings (Freed 1981; Nagy *et al.* 2007). Other temporal factors that affect body mass include diurnal variation and migration (Winker *et al.* 1992; Cresswell 1998; Schaub and Jenni 2000).

Black-capped Chickadee (*Poecile atricapillus*), a tree-foraging species, overcomes the hardships of winter by caching its resources (Sherry and Vaccarino 1989), relying on micro-climates (Cooper and Swanson 1994), undergoing facultative diurnal hypothermia (Lewden *et al.* 2014), and increasing breast muscle size and enzymatic activity to improve shivering thermogenesis (Liknes and Swanson 2011). In ground-foraging birds, the trend of adaptive winter fattening holds true for several species, including juncos and sparrows (King

and Farner 1966; Newton 1969; Rogers 1995), which those authors argued was exacerbated in ground-foragers because snowfall could limit access to ground-borne resources, resulting in food shortages. In comparison, tree-foraging species have more predictable resources, and as such do not need to build up as large a fat supply (Rogers 1987; Rogers and Smith 1993; Graedel and Loveland 1995). The body mass of tree-feeding species varies diurnally and seasonally, although the role of adaptive winter fattening is less prominent (Dawson and Marsh 1986; Silverin *et al.* 1989; Koivula *et al.* 1995; Cooper 2007).

There are several challenges associated with measuring size-corrected body mass in a non-destructive manner, such that ecologists have created various “condition indices” (Sears 1988; Redfern *et al.* 2000; Stevenson and Woods 2006; Jacobs *et al.* 2012). Some of the first indices involved using the ratio of body mass to a metric of body size, such as wing length. However, that method is often inaccurate because body size is seldom directly proportional to body mass (Peig and Green 2009). Calculating residuals from ordinary least squares regression (OLS) is one of the most popular methods, although several have argued that OLS violates key assumptions, leading to Type I and Type II errors (Garcia-Berthou 2001; Green 2001; Peig and Green 2009, 2010). To counter the flaws in OLS, Peig and Green (2009) developed the scaled mass index (SMI), which accounts for covariation between body size and body mass components during calculations by correcting body mass by a relative measure of body length.

Black-capped Chickadees are generally a well-studied species, particularly for food-storing behaviours (Sherry and Vaccarino 1989; Hitchcock and Sherry 1990; Smulders *et al.* 2004), social behaviour (Otter *et al.* 1998; Mennill *et al.* 2003), and vocal communication (Otter *et al.* 1997; Christie *et al.* 2004; Mennill and Ratcliffe 2004). The overall aim of our research was to provide additional information on fat mass variation at short- and long-time scales in Black-capped Chickadees using a 12-year data set and build on previous work that had focussed primarily on changes in muscle mass throughout the year (Swanson and Olmstead 1999; Swanson and Liknes 2006; Petit and Vézina 2014). Although we have direct estimates of visual lipid deposits within our dataset, those visual estimates are subjective and likely influenced by observer bias. Consequently, we elected to use a size-corrected mass index to estimate lipid levels in chickadees, with fat being the major cause of variation in body mass mediating a trade-off between higher reserves (longer fasting duration) and lower load (quicker predator escape). Thus, our first goal was to identify which condition index (body mass only, body mass/wing length, OLS, and SMI), is the most accurate predictor of lipids (as estimated by fat scores) in wild Black-capped Chickadees. We predicted that SMI would be the most reli-

able predictor of fat scores, as SMI accounts for proportions relative to the individual and overcomes the flaws found in OLS. Our second goal was to determine the trends in size-corrected body mass using the available data, through the comparison of the most reliable condition index with various predictors, including mean temperature, time of day, and age. As chickadees are an overwintering species, we predicted that at longer time-scales (months) they undergo adaptive winter fattening. Specifically, we predicted that chickadees would have a higher relative body mass in winter and lower relative body mass in summer. We also predicted that at shorter time scales (hours) chickadees would be lightest in the morning after a night of fasting and would increase in relative body mass through the day due to foraging (Bednekoff and Krebs 1995; Cresswell 1998; Kullberg 1998). Lastly, we predicted that older chickadees, which are more experienced at finding food, and typically of higher rank with better access to food, would need smaller fat reserves (Daunt *et al.* 2007; Marchetti and Price 2008).

## Methods

Data were collected in southern Quebec, Canada, at the McGill Bird Observatory from September 2004 until December 2015 as part of banding operations. The bird banding station is located adjacent to the Morgan Arboretum in Sainte-Anne-de-Bellevue, Quebec (45.43°N, 73.94°W), in an open mixed deciduous/coniferous forest. Black-capped Chickadees were caught in a total of 16 mist nets to be weighed, measured, aged, sexed, and banded by trained individuals. Mist nets (110d/2 thread, 30 mm, 4 shelf passerine nests from SpiderTech, Helsinki, Finland) measured 8–12 m in length, 3 m in height, with a mesh size of 30 mm. During the spring and fall migration monitoring period, mist nets were open for five hours daily, starting 30 minutes before dawn except during rain. During the summer, chickadees were captured during MAPS (Monitoring Avian Productivity and Survivorship) operations, with mist nets open for six hours daily, starting 30 minutes before sunrise for each 10-day period (DeSante *et al.* 2016). During the non-standard winter banding, mist nets were employed opportunistically based on the weather conditions. Birds were collected from nets every 30 minutes, or more often during windy days. To reduce the impact on the birds, we did not net in the rain or in very poor conditions, and consequently we may be unable to detect the effect of extreme conditions. Further information about the banding process appears in Gahbauer and Hudson (2014).

The resulting dataset contains 4459 observations from 1866 individuals with outliers (outliers = body weight or wing chord  $\pm$  4 SD) removed over the 12-year period. Outliers were likely due to human error during the recording of data. Black-capped Chickadees were aged by variation in their plumage. Not all individuals were reliably aged, depending on the time of

year and the plumage characteristics, and in these cases the birds were recorded as unknowns (Pyle 1997). Chickadees were assigned “young” and “old” age classifications. Birds of unknown age were excluded from the analysis. Fall hatch-year and spring second-year birds were categorized as “young” and fall after hatch-year and spring after second-year were considered “old”, for a total of 4248 observations that were of known age (Table 1). We did not determine the sex of the birds outside of the breeding season, so it was excluded from the analyses. Birds were weighed on an electronic balance (iBalance 700, My Weight Canada, Vancouver, British Columbia, Canada; accuracy of 0.1 g), and wing length was measured with a ruler (accuracy of 1 mm). Each bird was released shortly after the banding process was completed.

Subcutaneous fat was visually estimated using standard protocol and codes from the MAPS program (DeSante *et al.* 2016). As described by Rogers (1991: 351):

Each bird was held in the left hand, ventral side up, with the first two fingers of the left hand on the ventral (first finger) or dorsal (second finger) side of the neck. The first finger pressed against the base of the bill so that the bill pointed forward at approximately 45° above the extended longitudinal axis of the bird. The first finger of the right hand was held lightly against the left side of the pectoral musculature while the right thumb lightly held the tail in its natural position. Birds were held gently to avoid injury, but firmly to avoid escape. With the bird held in the above position, the ventral contour feathers were blown aside and the subcutaneous fat observed in the two defined areas was classified as follows (after Nolan and Ketterson 1983). 0 = no visible fat on abdomen (A) or in furcular depression (F). 1 = F < 33% full, A < 50% covered. 2 = F 33–66% full, A 50–100% covered but fat layer not even with pectoral region. 3 = F filled and fat flush with pectoral musculature, A completely covered, fat layer flush with pectoral musculature, thus neither F nor A bulging outward from pectoral musculature. 4 = as in 3 with F or A bulging. 5 = both F and A bulging. Subcutaneous fat was recognized by its yellow or orange-yellow color, which contrasts with the dark red color of muscle.

Temperature data were collected from the Sainte-Anne-de-Bellevue climate station, located 1.5 km away from the banding sites (45.25°N, 73.55°W), in Sainte-Anne-de-Bellevue, Quebec, Canada. As temperature data were occasionally missing from the local climate station, missing data were replaced using an equation (Sainte-Anne-de-Bellevue Temperature = 0.9987 ×

**TABLE 1.** Number of captures of Black-capped Chickadees (*Poecile atricapillus*) across a 12-year period in southern Quebec, Canada. Only those used in the analyses are included ( $n = 4248$ ). Seasonal captures across all years were: 332 in late winter (January–March), 297 in spring (April–May), 542 in summer (June–August), 2277 in fall (September–October), and 800 in early winter (November–December).

Year	Number of captures
2015	393
2014	379
2013	272
2012	551
2011	342
2010	711
2009	331
2008	164
2007	307
2006	229
2005	442
2004	127

Airport Temperature – 0.2886,  $R^2 = 0.99$ ) based on available data from the next closest climate station, at the Pierre Elliott Trudeau Airport (16 km away from banding sites; 45.28°N, 73.45°W) in Montréal, Quebec, Canada (Environment Canada 2015).

#### Comparing condition indices

The regressions of the log-transformed body mass and wing length were taken to determine the slope of the regression (1.105), which was used later during the SMI calculations. We used a linear mixed-effects model (R package nlme; function lme; Pinheiro *et al.* 2016) to compare four different measurement methods: body mass only, body mass/wing length, OLS, and SMI, all of which act as predictors of fat. The data included only the individuals that had been captured at least three times over the duration of the study (2787 observations from 360 individuals) and using a linear mixed-effect model reduced pseudo-replications associated with recaptures. “Body mass only” used the actual weight (g) of each bird recorded by banders. We calculated the “weight/wing length” for each individual by dividing body mass (g) by wing length (mm). We obtained OLS values by calculating the residuals of body mass on wing length using the ordinary least squares regression. SMI was calculated using the formula

$$\widehat{M}_i = M_i \left[ \frac{L_o}{L_i} \right]^{b_{SMA}}$$

where slope (1.105) of the body mass ~ wing length regression acted as the scaling exponent,  $b_{SMA}$ , and  $M_i$  and  $L_i$  were the observed values,  $L_o$  was the average length value for the entire population, and  $\widehat{M}_i$  was the predicted value for mass (Peig and Green 2009). Prior to using parametric statistics, we tested for normality in the data (Shapiro-Wilks; cut-off of  $W > 0.95$ ; R package stats; function shapiro.test; R Core Team 2015).

We excluded fat scores of 4, 5, or 6 due to very small sample sizes, and because the average mass for 4, 5, and 6 were lower than the average fat score of 1, thereby implying they were likely erroneous (i.e., chickadees are never fatter than a 3). The excluded values were distributed randomly throughout the year, and showed no pattern (and were rare), so excluding these values had no impact on our results. Because fat scores do not linearly translate into body mass, we first converted fat into body mass using the same model with fat score as a function of body mass (fixed effect) and individual (random effect), only including those individuals with at least three measurements. Setting a fat score of zero equal to 0 g, based on the linear effects model, a fat score of one was equal to 0.14 g, a fat score of 2 was equal to 0.39 g, and a fat score of 3 was equal to 0.54 g. Next, for each condition index, we calculated a linear mixed-effect model of fat score (converted to mass as above and with fat scores greater than 3 excluded) as a function of condition (fixed effect) and individual (random effect). We used Pearson's product-moment correlation test (R package *stats*; function *cor*; R Core Team 2015) to determine whether wing length is independent of body mass. We used a significance test with alpha set at 0.05 to determine which variables to include in the linear mixed-effect models.

#### *Predictors of variation in size-corrected body mass*

We calculated SMI for all 4248 observations for further analyses to test various predictors: temperature, age, and time of capture as time of day, and time of capture in month and years. We corrected for the time of day of capture by sunrise, using the formula: (time of capture – time of sunrise)/day length. Sunrise and day length data were collected from the National Research Council's sunrise database (National Research Council Canada 2016), using Montréal as the closest available city. Time of capture in month and year for all analyses were treated as categorical variables.

We first explored the relationships between the five possible drivers of SMI individually using univariate tests. For age (old versus young) we ran an unpaired, one-sample t-test (R package *stats*; function *t.test*; R Core Team 2015). For temperature and relative time capture we used linear regression (R package *lm*; function *t.test*; R Core Team 2015). For month and year of capture we use an analysis of variance (R package *aov*; function *t.test*; R Core Team 2015).

Next, we determined the relative strength of each driver, or biologically relevant combination of drivers, using mixed-effect linear models (R package *lme4*; function *lmer*; Bates *et al.* 2017), with individual as a random effect. We framed our *a priori* candidate models to test the following hypotheses: (1) including all drivers (temporal, temperature, age) effects additively (global model), (2) average hourly temperature of the capture time alone (temperature model), (3) age of the individual at the time of capture alone (age model), (4) shorter time-scale temporal effects only as capture time of day alone (time of day model), (5) longer time-scale temporal effects including additive effects of month and year of capture (month/year model), (6) longer time-scale temporal effects including additive and interaction effects of month and year of capture (interaction month/year model), (7) short and long time-scale effects together additively (time of day/month/year model), and (8) short and long time-scale effects together additively, and interaction of month and year of capture (interaction day/month/year model). We evaluated all nine models (including a null model with random effect of individual only) using Akaike Information Criterion adjusted for small sample sizes (AICc; Hurvich and Tsai 1989). Models were ranked according to the strength of support of each model, as determined by the difference in AICc between a given candidate model and the model with the lowest AICc ( $\Delta$ AICc; Anderson *et al.* 2001). AICc is a measure of model performance, which compares the maximum-likelihood estimates of the models, while penalizing for increasing complexity. Ranking was corroborated with the conditional  $R^2$  of the models (R package *piecewiseSEM*; function *sem.model.fits*; Lefcheck 2016).

## Results

### *Comparison of condition indices*

SMI was the best predictor for subcutaneous fat measured in Black-capped Chickadees ( $t_{2423} = 5.05$ ;  $P < 0.0001$ ), followed by body mass only, body mass/wing length, and OLS (Table 2). Pearson's product-moment correlation test showed that wing length correlated positively with body mass ( $t_{2423} = 43.7$ ,  $P < 0.0001$ ,  $R = 0.55$ ).

### *Predictors of SMI in Black-capped Chickadees*

We found no significant difference between the SMI of young versus old Black-capped Chickadees (Figure 1a), with older birds having an average SMI of

**TABLE 2.** Simple regression statistical output for four different body condition indices as predictors of fat in Black-capped Chickadees (*Poecile atricapillus*) captured across a 12-year period in southern Quebec, Canada. Shown are the computed standard error, *t*-value, and *P*-value from a linear mixed effects model.

Model	df	<i>t</i> -value	<i>P</i> -value
Body mass only	2423	4.04	0.0001
Body mass/wing length	2423	-1.67	0.1000
Ordinary least squares regression	2423	1.59	0.1100
Scaled mass index	2423	5.05	<0.0001

10.90 ± 0.62 (SD) g, and young birds having an average of 10.92 ± 0.60 g. While both regressions of temperature and the relative time of capture to SMI were significant ( $P < 0.001$ ), both model fits were low (Adjusted  $R^2 = 0.03, 0.005$ , respectively; Figure 1). Overall, SMI of Black-capped Chickadees decreased with increasing temperature (Figure 1b) and increased with relative time of capture (Figure 1c). SMI of Black-capped Chickadees also significantly differed across the 12 months of the year, and the 12 years of the study (Figures 1d,e).

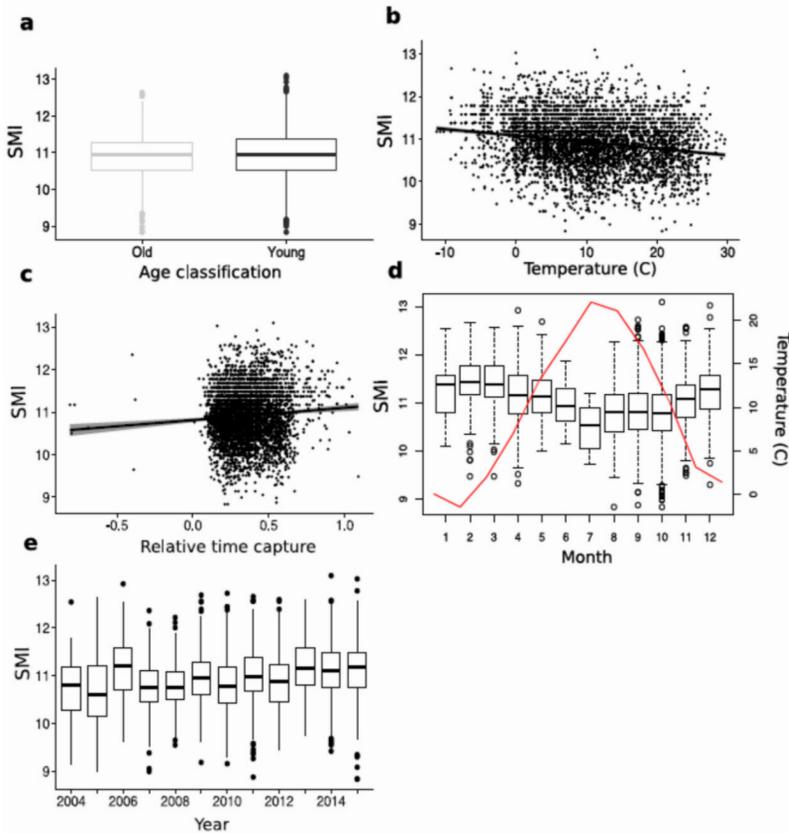
Of the nine models tested, the model that included all the temporal variables (time of day of capture, month, and year) explained the most variation in the SMI of Black-capped Chickadees (Table 3). The next best model (month/year of capture, as determined by AICc) was >8 AICc from the top model, thus it was significantly weaker than the top model (Anderson 2008). Thus, SMI variation in Black-capped Chickadees was primarily driven by temporal factors. We found a signif-

icant and positive effect of the time of day, with birds increasing in SMI later in the day (Table 4). Chickadees varied in their SMI across the year, with birds later in the winter (February and March) having significantly greater SMI, and birds in the later summer and fall (July–November) having significantly lower SMI, compared to a January baseline (Table 4). SMI also varied across the 12-years of study, with certain years (e.g., 2013–2015) having chickadees with significantly higher SMI on average (Table 4).

## Discussion

### *SMI as an indicator of fat stores in Black-Capped Chickadees*

As predicted, SMI was the most accurate predictor of subcutaneous fat stores in Black-capped Chickadees, followed by body mass only, and body mass/wing length. OLS correlated the least to fat stores. Our results support our prediction that SMI, which corrects body mass by relative wing length, would be the most accu-



**FIGURE 1.** a. Boxplot of scaled mass index (SMI) of young and old Black-capped Chickadee (*Poecile atricapillus*); b. scatterplot of SMI versus mean temperature of day of capture for Black-capped Chickadees with linear regression line and 95% confident region in grey; c. scatterplot of SMI versus relative time of capture for Black-capped Chickadee; d. boxplots of SMI of Black-capped Chickadee across 12 months of the year, averaged across all years of study, with line graph of the average monthly temperature for each month across the study period in red; e. boxplots of mean SMI of Black-capped Chickadees across 12 years of the study.

**TABLE 3.** Summary of rankings of candidate models using Akaike Information Criterion for small sample sizes (AICc) from linear mixed-effects models assessing the variation of scaled mass index (SMI) in Black-capped Chickadees (*Poecile atricapillus*) captured across a 12-year period in southern Quebec, Canada.

Model	df	$\Delta$ AICc	Conditional R <sup>2</sup>
Time of day/month/year	26	0.0	0.67
Month/year	25	53.9	0.67
Global	113	151.7	0.69
Interaction time of day/month/year	111	182.7	0.69
Interaction month/year	110	232.2	0.68
Temperature	4	509.2	0.61
Time of day	4	577.3	0.62
Age	4	646.2	0.60
Null	3	663.7	0.59

**TABLE 4.** Parameter estimates from the time of day/month/year linear mixed-effects models assessing the variation of scaled mass index (SMI) in Black-capped Chickadees (*Poecile atricapillus*) captured across a 12-year period in southern Quebec, Canada. Model output for month effects are relative to January, and year effects relative to 2004. Significant parameter estimates are bolded.

Model parameters	Estimates	SE	Df	<i>t</i> -value	<i>P</i> -value
<b>Time of capture</b>	0.36	0.04	3268	7.80	<0.001
Month of capture					
<b>February</b>	0.15	0.07	3423	2.07	0.040
<b>March</b>	0.15	0.06	3397	2.36	0.020
April	-0.03	0.07	3410	-0.49	0.630
May	0.06	0.07	3324	0.84	0.400
June	-0.13	0.11	3763	-1.12	0.260
<b>July</b>	-0.75	0.09	3587	-8.45	<0.001
<b>August</b>	-0.42	0.06	3492	-6.83	<0.001
<b>September</b>	-0.37	0.06	3502	-6.12	<0.001
<b>October</b>	-0.36	0.06	3561	-6.16	<0.001
<b>November</b>	-0.21	0.06	3436	-3.55	<0.001
December	-0.06	0.06	3323	-0.89	0.370
Year of capture					
2005	-0.08	0.05	3930	-1.54	0.120
<b>2006</b>	0.20	0.06	4036	3.10	<0.001
2007	0.02	0.06	4227	0.31	0.760
2008	0.05	0.07	4200	0.67	0.510
<b>2009</b>	0.14	0.06	4218	2.30	0.020
2010	-0.02	0.06	4161	-0.41	0.690
<b>2011</b>	0.13	0.06	4228	2.03	0.040
2012	0.10	0.06	4149	1.72	0.090
<b>2013</b>	0.28	0.07	4202	4.23	<0.001
<b>2014</b>	0.26	0.06	4123	4.05	<0.001
<b>2015</b>	0.18	0.07	4029	2.75	0.010

rate condition index out of the four methods for Black-capped Chickadees. Similar to our findings, SMI was found to be a good predictor in another passerine species, European Starling (*Sturnus vulgaris*; Peig and Green 2009), while being a poor predictor of fat stores in non-passerine birds (Jacobs *et al.* 2012).

The use of OLS as a measure of body condition has been contested in recent years (Labocha and Hayes 2012). Peig and Green (2009) argued that OLS favours large individuals, as OLS measures absolute rather than relative fat (see Blackburn and Gaston 1997). Moreover, OLS may lead to Type I and Type II errors via violations of key assumptions—that the body size indicator (BSI) length (in this study: wing length) is

independent of mass, and that BSI length does not have error (Green 2001). The result from the Pearson's product-moment correlation test demonstrates that our data violates the first assumption. Conversely, Schulte-Hostedde *et al.* (2005) compared OLS to major axis and reduced major axis regression and found OLS to be the suitable choice. Likewise, Jacobs *et al.* (2012) found that OLS outperformed SMI in predicting lipid stores in seabirds. While “body mass only” was the second most reliable option, we do not recommend using body mass alone as a predictor of fat *in lieu* of other methods, as it is necessary to account for relative proportions of each individual.

*Temporal drivers as strongest predictors of SMI variation in Black-Capped Chickadees*

Temporal variables at both short time-scales (hours of the day) and long time-scales (months and years), were the strongest predictors of SMI variation in the Black-capped Chickadees in our study area. SMI was lowest in the morning and higher later in the day, which supports our prediction. Black-capped Chickadees spend several hours in the morning foraging to compensate for the energy lost the previous night. As hours go by, mass will increase until nightfall arrives again and body mass drops (Brittingham and Temple 1988). As shown in other studies, plasma triglycerides, indicative of fattening, are also high through mid-morning before dropping off in the afternoon, implying that most fattening occurs in the early morning (Mandin and Vézina 2012; Devost *et al.* 2014). Triglyceride levels, and therefore fattening, are highest in mid-winter (Mandin and Vézina 2012), consistent with our study.

SMI was, averaged across years, lowest from July to November, and highest in January to March suggesting that Black-capped Chickadees undergo adaptive winter fattening, although seasonal variation in body mass may be stress-induced or adaptive in other ways (Ketterson *et al.* 1991; Cresswell 1998; Kitaysky *et al.* 1999; Thomas 2000; Krams *et al.* 2009; Ratikainen and Wright 2013). Lower body mass in summer may be attributed to the stress of breeding season (Nagy *et al.* 2007), or reduction in energetic demands when flying to facilitate delivery of food to nestlings (Freed 1981; Croll *et al.* 1991). However, as we found low SMI from July–November, including the period well outside of the breeding season, we suggest that changes in SMI are mostly associated with winter fattening. Interestingly, we found that mean temperature did not significantly affect SMI in chickadees despite the seasonal variation in body mass. This discrepancy suggests that fat mass is programmed to increase during winter, rather than in response to immediate ambient temperature, although other factors, such as food availability and predation risk, may play important roles. These results are similar to other studies on tree-foraging species, including American Goldfinch (*Spinus tristis*; Dawson and Marsh 1986), Great Tit (*Parus major*; Silverin *et al.* 1989), and Willow Tit (*Poecile montanus*; Silverin *et al.* 1989; Koivula *et al.* 1995).

Age did not significantly affect SMI. In other species, weight generally increases with age due to growth and perhaps an improvement in feeding efficiency (Brooke 1978; Weimerskirch 1992). However, previous work on chickadees has demonstrated that birds of higher rank, which tend to be older (3.2 y compared to 1.5 y for subordinates), are often lighter with lower fat scores, presumably because they have better access to food sources (Schubert *et al.* 2007). We expected younger birds, presumably of lower rank, to have a higher SMI to buffer against the risk of starvation, a threat which

might be greater for younger birds, but our data do not reflect this.

Black-capped Chickadees are often the focus of food-caching research, but there are few data on predictors and mechanisms behind body mass variation in this species. Although chickadees demonstrated winter fattening, it remains to be seen if temperature acts as a proximal or ultimate cause of weight gain/loss. The next step is to undertake experimental manipulations of temperature to determine how that influences avian body mass. Past studies have demonstrated that temperature, when measured over a longer period of time (e.g., several days to a month), acts as a proximal influence on metabolic rate in chickadees (Swanson and Olmstead 1999; Dubois *et al.* 2016). This current study used a much smaller window (time of capture) to assess the impact of temperature, and thus future research may wish to examine longer temporal variables as potential proximate factors.

### Author Contributions

Writing – Original Draft: E.N.; Writing – Review & Editing: K.E. and B.F.; Data Collection: B.F.; Formal Analysis: E.N., B.F., and K.E.

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