

## Research

### Does habitat fragmentation promote climate-resilient phenotypes?



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Understanding how individual differences in physiological performance modify behavioral responses to environmental variability and its fitness consequences is key to predicting the vulnerability of species and populations to environmental change. For many species, summit metabolic rate ( $M_{SUM}$ ; the upper limit to heat production) and basal metabolic rate (BMR; the lower limit related to energy acquisition and processing) often constrain aspects of physiological performance and behavioral activity. We examined the relationship between metabolic phenotypes, foraging behavior, and survival in overwintering black-capped chickadees *Poecile atricapillus* inhabiting contiguous and fragmented forested landscapes. We found that birds with lower summit metabolic rates were generally more sensitive to winter weather and increased their use of supplemental feeding stations as ambient temperatures decreased. In highly fragmented forests, this relationship may have incurred strong survival consequences, as birds with lower summit metabolic rates were less likely to survive the winter season. Additionally, we found that chickadee populations persisting in fragmented landscapes were characterized by slightly higher thermogenic capacity ( $M_{SUM}$ ) and lower maintenance metabolic costs (BMR). We suggest that habitat loss and fragmentation present unique selection pressures that alter the relationships between environmental variability, behavior and physiology, and result in context-specific fitness consequences.

Keywords: habitat fragmentation, foraging behavior, metabolism

Synthesis

Climate change and habitat fragmentation are the two greatest threats to biodiversity, yet a critical question remains as to whether populations can adapt to these changes and which phenotypes will be favored over time. In this study, winter birds depended more on supplemental food during poor weather, but this dependency reflected their capacity to generate heat. Birds in fragmented forests had higher thermogenic capacity, lower basal metabolic rates, and were subsequently less sensitive to climate variability. Habitat fragmentation could produce climate-resilient phenotypes, but we need more studies on how individual behavior and physiology mediate species' responses to environmental change.



## Introduction

Energy metabolism is an important variable in animal ecology as it connects processes across multiple levels of biological organization and mediates how individuals and species respond to environmental change (Brown et al. 2004). Within species, metabolism is an important driver of individual responses to environmental variability (Careau and Garland 2013). Across species, metabolic constraints have been invoked to explain broad-scale patterns of species distribution and abundance (Anderson and Jetz 2005, Buckley et al. 2012). Therefore, as species are increasingly faced with rapid environmental changes, metabolism is a potentially critical component determining how individuals interact with their environment with important population-level consequences (Burton et al. 2011).

Physiological constraints often limit behavioral responses to environmental changes (Burton et al. 2011). For example, in an experimental study on deer mice *Peromyscus maniculatus*, individuals with a higher upper limit to heat production ( $M_{\text{SUM}}$ ) remained relatively more active under colder conditions (Sears et al. 2009). Similarly, zebra finches *Taeniopygia guttata* with high basal metabolic rates (BMRs) were more energetically constrained and made significantly greater use of a foraging tactic that reduces uncertainty in resource gains (scrounging) than low BMR birds (Mathot et al. 2009). While metabolic constraints may mediate behavioral responses to environmental changes, it is unclear whether, and under what ecological conditions, these differences in behavior have consequences on survival or other measures of fitness. Because individual variation in phenotypic traits provide the raw material for natural selection to act on (Bolnick et al. 2003), a critical question is whether populations can adapt to rapid environmental changes, and if so, which phenotypes will be selected for over time (Parmesan 2006). Additionally, birds may flexibly alter their responses to environmental change and lessen the necessity for rapid adaptation (Piersma and van Gils 2011). Consequently, understanding the physiological and behavioral responses of birds across different environmental contexts, and its impact on survival, is critical to our understanding of how species will respond to future anthropogenic changes (Crispo et al. 2010).

Wintering birds provide ideal subjects to examine the influence of environmental variability on the interaction between physiology, behavior, and survival due to their small body size, increased energetic demands, and propensity to use supplemental food. Birds exhibit seasonal increases in both  $M_{\text{SUM}}$  and BMR during the winter-acclimatization process, but the mechanisms underlying this metabolic flexibility are thought to be different (Swanson and Vézina 2015). Whereas,  $M_{\text{SUM}}$  is primarily influenced by the size of pectoralis muscles used in shivering thermogenesis (Cooper 2002, Petit and Vézina 2014), variation in BMR is largely determined by the size and activity of tissues used for energy acquisition and processing (McKechnie and Swanson 2010).

During the winter, BMR can comprise up to 50% of an individual's energy budget (Sgueo et al. 2012), and foraging activity is expected to correlate with BMR (Careau et al. 2008). In great tits *Parus major*, birds with high BMRs were quicker to resume feeding at bird feeders following a simulated predator attack (Mathot et al. 2014). Additionally, female great tits with high BMRs were less active, and explored their environment less when placed in a novel setting (Bouwhuis et al. 2014). Together, these results suggest that energy constraints imposed by high BMR may limit the ability of birds to adjust foraging behaviors (Bouwhuis et al. 2014, Mathot et al. 2014). However, this relationship likely depends on whether BMR imposes a considerable constraint on the allocation of energy towards activity (Mathot and Dingemanse 2015).

As metabolic rates are a function of tissue properties, it has recently been suggested that greater activity levels in birds should be more tightly coupled with  $M_{\text{SUM}}$  rather than BMR because of the higher contribution of skeletal muscle size and activity in generating maximum metabolic capacities (Wagner et al. 2013). This can be seen in cross-training experiments where both exercise-induced and cold-induced maximum metabolic rates are driven by skeletal muscle mass (Zhang et al. 2015). Therefore, physiological adjustments that promote enhanced thermogenic capacities might influence whether an individual is willing or able to forage under cold conditions (Sears et al. 2006), with implications for overwinter survival (Petit et al. 2016).

In winter, birds must simultaneously balance the risks of starvation and predation; as temperatures decrease, individuals may increase foraging rates, at the risk of increased predation rates (Lima 1986). Thus, foraging activities necessarily impose tradeoffs between energy intake and survival and are further confounded by habitat fragmentation (Villafuerte et al. 1997, Evans 2004). For example, fragmentation can modify energy demands resulting from altered microclimates (Dolby and Grubb 1999, Turcotte and Desrochers 2003, Olson et al. 2013), reduced food supply (Doherty and Grubb 2003), and higher predation risk (Turcotte and Desrochers 2003). Importantly, while human-provided food resources can buffer the negative impacts of winter conditions (Brittingham and Temple 1988), it may not be sufficient to counteract these effects in highly fragmented landscapes (Doherty and Grubb 2003). Consequently, gradients in habitat fragmentation may alter selection pressures that act to simultaneously minimize maintenance metabolic costs while maximizing thermogenic capacity, resulting in a higher absolute aerobic scope (AAS;  $M_{\text{SUM}} - \text{BMR}$ ).

Our goal was to explore the interactions between physiology, behavior, and survival of wintering birds within human-modified landscapes. To do so, we examined the relationships between individual variation in  $M_{\text{SUM}}$  and BMR, and foraging activity of black-capped chickadees *Poecile atricapillus* within contiguous and fragmented forested landscapes. We hypothesized that, at a population level, birds in fragmented

landscapes would have lower BMR resulting from fewer resources, and higher  $M_{SUM}$  associated with increased thermoregulatory demands. At an individual level, we hypothesized  $M_{SUM}$  would be a better predictor of foraging activity than BMR, and that birds with higher  $M_{SUM}$  would use bird feeders more often throughout the winter. Additionally, as a higher  $M_{SUM}$  could afford individuals the opportunity to be more active under cold conditions, we predicted birds with high  $M_{SUM}$  would increase their feeder use to a greater extent on cold days, resulting in greater sensitivity to temperature variability. Lastly, because of its connection with cold endurance, we expected  $M_{SUM}$  would be positively related to overwinter survival, particularly in fragmented forests. Examining the relationship between energy metabolism and behavior within human-modified landscapes provides a unique exploration of the consequences of environmental variability on animal ecology and demographics.

## Material and methods

### Study populations

Our study sites consisted of four forested woodlots embedded within a predominately agricultural matrix in Dane County, Wisconsin. We chose these plots to represent two ends of a forest fragmentation gradient (Fig. 1; Supplementary material Appendix 1 Table A1) that was previously shown to have strong differences in winter microclimates, with forest woodlots in more fragmented landscapes experiencing prolonged exposures to cold temperatures (Latimer and Zuckerberg 2017). The four sites were spaced 34 km apart on average ( $\pm 19$  km SD). We selected plots to minimize the impact of other supplemental food sources on bird behavior such that the nearest human dwelling was  $> 1$  km away, larger than the average winter home range size of a black-capped chickadee (Smith 1991). In addition, nearby property owners agreed to not feed birds for the duration of the study.

### Food provisioning and RFID monitoring

In August of 2013, a single bird feeder equipped with a low-cost radio frequency identification (RFID) reader, described in detail elsewhere (Bridge and Bonter 2011), was placed in the center of each plot. Feeders were consistently filled throughout the first winter (2013/2014) to ensure birds would become habituated to the presence of the feeder before the start of this study. Feeders were set to poll for passive integrated transponder (PIT) tags every 5 s with a poll interval duration of 300 ms. During the winter of 2014/2015, each feeder was filled with black-oil sunflower seeds every two days from October through March. We placed a microclimate sensor ( $0.5^\circ\text{C}$  resolution) at each feeder location and recorded temperatures at half-hour intervals. We captured birds at feeders continuously throughout the winter using mist nets, and affixed 2.3 mm colored plastic leg band fitted with a PIT tag from IB technology (model number



Figure 1. Two extremes of the forest fragmentation gradient considered in this study. The landscape in (A) is comprised of 7% forest cover, whereas the landscape in (B) is comprised of 80% forest cover. Red dots indicate the location of the bird feeder within the center of each forest patch.

EM4102). Every time a PIT-tagged bird landed on a feeder, its unique identifier, date, and time were recorded by the RFID reader. Chickadees typically grab a seed from a feeder and fly to a nearby perch to consume it (Smith 1991). Therefore, we assume that each single visit recorded by the feeder corresponds to one seed being taken and eaten or cached for later consumption. After capture, birds were weighed and measured following standardized protocols (length of head

plus beak, tarsus and wing). We used the shape and wear of the sixth retrices to determine the age (young or adult) of each bird (Pyle 1997).

### Metabolic measurements

In February and early March 2015, we captured birds at feeders around dusk (14:00 h) and brought them into the lab for metabolic measurements. We restricted access to food for four hours prior to BMR measurements to ensure birds were in a fasted state. Black-capped chickadees brought into the laboratory were weighed ( $\pm 0.1$  g) and placed in individual, airtight, 1-liter glass metabolic chambers inside a dark, temperature-controlled cabinet with no access to food or water beginning at 19:00 h. To monitor ambient temperature ( $T_a$ ) within the chambers, a 30-gauge copper-constantan thermocouple was inserted. Each chamber contained a wire mesh platform above a thin layer of mineral oil to capture feces and eliminate them as a source of water vapor. For BMR measurements, we kept temperature cabinets at 29°C, which is within the thermoneutral zone of a black-capped chickadee (Chaplin 1976). Dry, CO<sub>2</sub> free air was pumped through the metabolic chambers at rates between 330–345 ml min<sup>-1</sup> + 1% through a precision rotameter calibrated with a soap bubble meter. Excurrent air passed through a RH-100 humidity meter, through tubes containing drierite, ascarite, and another layer of drierite to remove water and CO<sub>2</sub>, and then through an oxygen analyzer to measure fractional concentration of oxygen. Outputs from the thermocouple, humidity meter, and oxygen analyzer were recorded every second using a UI-2 A/D converter with a Sable Systems multiplexer that allowed switching between two metabolic chambers at 15 min intervals. Measurements lasted for five hours at which point, birds were returned to their cages while two more birds underwent the same procedure. Mass and body temperature of each bird was recorded before and after each trial. We calculated the rate of O<sub>2</sub> consumption following (Lighton 2008). BMRs are reported as minimum 10-min averages from the BMR trial. The following morning, approximately one hour before sunrise, we started the M<sub>SUM</sub> trials. Prior to the start of M<sub>SUM</sub> trials, we switched the air flowing through the chambers to a mixture of 21% oxygen and 79% helium (helox) and decreased the temperature in the cabinet to -10°C. We conducted M<sub>SUM</sub> trials at a constant temperature of -10°C because previous research indicates that winter-acclimatized black-capped chickadees generally become hypothermic in a helox environment at temperatures below -9°C (Cooper and Swanson 1994). Only a single M<sub>SUM</sub> was recorded at a given time, and food was withheld throughout the duration of the trials. The purpose of using helox was to reduce the thermal conductivity of the birds so they lose heat more readily to the environment (Rosenmann and Morrison 1974). We recorded the oxygen consumption of each bird during cold exposure and ended the trial when birds became hypothermic (O<sub>2</sub> consumption decreased steadily for 3 min without subsequent increase), or after 75 min of cold exposure. All values of oxygen consumption were calculated using Warthog Systems

LabAnalyst X. We obtained measurements of body mass ( $\pm 0.1$  g) before and after and body temperature ( $T_b \pm 0.1^\circ\text{C}$ ) after each trial.  $T_b$  was recorded ( $\pm 0.1^\circ\text{C}$ ) with a thermocouple thermometer and 30-gauge copper-constantan thermocouple. We assumed a bird had reached its M<sub>SUM</sub> when body temperature after the trial was  $\leq 38^\circ\text{C}$  (Swanson et al. 1996). Mean body temperature after the M<sub>SUM</sub> trials was  $36.9 \pm 0.4^\circ\text{C}$  with 17 (65%) of individuals reaching hypothermia. We therefore assume that -10°C was sufficient to produce M<sub>SUM</sub> (Swanson et al. 1996). Upon completion of the M<sub>SUM</sub> trials, we returned the birds to their cages with access to food and water ad libitum until they were later released at the site of capture. All birds recovered from hypothermia after these trials and were recorded at feeders for at least one week after release. We then determined the AAS for each individual by subtracting M<sub>SUM</sub> from BMR.

### Statistical analyses

We used analysis of covariance (ANCOVA) to test for population-level differences in metabolic phenotypes between contiguous and fragmented landscapes, while controlling for potential differences in average temperatures 30 days prior to metabolic measurements and differences in body mass between populations. Fat scores were higher in birds that were captured in fragmented landscapes (Mann–Whitney U-test  $W = 92$ ,  $p = 0.034$ ), so we opted to use wing length instead of body mass to account for size differences since fat is largely metabolically inactive (Lewden et al. 2012). For this purpose, we tested BMR, M<sub>SUM</sub> and AAS as the response variables, with fragmentation type (modeled as a categorical variable), daily minimum temperatures averaged over 30 days prior to metabolic measurements, and wing length as independent variables (Swanson and Olmstead 1999).

Because prior research on this species suggests that BMR is flexible within winters (Petit et al. 2013), and largely determined by minimum temperatures a month prior to measurements (Swanson and Olmstead 1999), we analyzed feeding rates (individual visits to feeders per day as an indicator of reliance on supplementary food) of individuals within one month centered on the time their BMR measurements were taken, beginning 1 January 2015 and ending 1 April 2015. Previous research in the same species found that BMR was repeatable within individuals throughout a given winter; whereas, M<sub>SUM</sub> was repeatable across winters (Cortés et al. 2015). Therefore, we assume that M<sub>SUM</sub> and BMR remained relatively unchanged within the one month window when measurements were taken.

We used generalized linear mixed-effects models (GLMM) with a Poisson distribution (Bolker et al. 2009) and individual ID nested within woodlot as random effects to control for the non-independence of individuals within the same woodlot, while examining the relationship between individual feeder use and BMR or M<sub>SUM</sub> separately. In this case, the random intercept for each individual represents the among-individual variation in average feeder use. Given concerns

about adequate levels of random effects (Harrison et al. 2017), we also included the analysis without woodlot as a random effect. To test for overdispersion in our data, we calculated a dispersion statistic as the ratio of the sum of squared Pearson residuals divided by residual degrees of freedom, which approximately follows a  $\chi^2$ -distribution (Zuur et al. 2013). Ratios greater than 1 indicate likely overdispersion (Zuur et al. 2013). Initial model runs indicated our data were highly overdispersed ( $\chi^2 = 11657$ ,  $df = 964$ ,  $p < 0.001$  for BMR and  $\chi^2 = 11641$ ,  $df = 964$ ,  $p < 0.001$  for  $M_{SUM}$ ), so we used an observation-level random effect (OLRE) to control for extra Poisson variance (Elston et al. 2001, Harrison et al. 2017). After inclusion of the OLRE, there was no further indication of overdispersion ( $\chi^2 = 161.8$ ,  $df = 963$ ,  $p > 0.9$  for BMR and  $\chi^2 = 161.8$ ,  $df = 963$ ,  $p > 0.9$  for  $M_{SUM}$ ). We did not include  $M_{SUM}$  and BMR as predictors in the same model because they were significantly correlated with each other ( $r = 0.45$ ,  $p = 0.04$ ). We tested the significance of random effects using a likelihood ratio test (LRT) between models with and without random effects. We included fragmentation type as a dummy variable (fragmented or contiguous), metabolic rate (BMR or  $M_{SUM}$ ), minimum temperature of the day prior (from the HOBO sensor), snow (in cm recorded from the nearest weather station) and wing length (an indicator of body size) as fixed effects. We used F-tests and t-tests to determine potential differences in the variances and means of average feeder visitation within each fragmentation type. Significant differences in means or variances would suggest that fragmentation type was a poor grouping variable. As neither variances nor means differed between woodlots in fragmented ( $F_{4,5} = 1.6$ ,  $p = 0.61$ ;  $t_9 = 0.15$ ,  $p = 0.88$ ) or contiguous ( $F_{5,4} = 3.1$ ,  $p = 0.31$ ;  $t_9 = 1.87$ ,  $p = 0.09$ ) landscapes, we kept fragmentation type as a categorical predictor in the models. We also included the interaction between metabolic rate and temperature to allow the slope of the relationship between feeding rate and temperature to change as a function of an individual's metabolism. A positive interaction would suggest birds with higher BMR or  $M_{SUM}$  were more sensitive to changes in ambient temperatures. Lastly, we included the two-way interactions for temperature and fragmentation to test for possible differences in the foraging response of birds to temperature in fragmented and contiguous landscapes. Because temperatures differed by  $2^\circ\text{C}$  on average between fragmented and contiguous landscapes, and were thus collinear with fragmentation type, we scaled temperature covariates by subtracting each observation by the mean and dividing by the standard deviation of each fragmentation class separately prior to modeling (Freckleton 2011). While sex and age can influence individual use of supplemental feeding stations (Crates et al. 2016), we were unable to determine the sex of individuals in this study, and models regularly failed to converge when age was included as a fixed factor. Therefore, we fit models with daily feeder visitation rate as a function of age to determine if there was any influence of age on individual feeder use throughout the winter (Supplementary material Appendix 1 Table A2). This analysis confirmed that feeder

use was not significantly related to age so we excluded age from further analyses. We assumed an  $\alpha = 0.05$  for significant results and  $\alpha = 0.10$  for marginally significant results.

We applied Cormack–Jolly–Seber (CJS) (Lebreton et al. 1992) models for capture–mark–recapture data within the modeling program MARK (White and Burnham 1999) to examine differences in apparent survival ( $\Phi$ ) among individuals. Apparent survival is a function of true survival and the probability of permanent emigration (Burnham 1993). We collapsed our feeding rate data from the entire winter into 18 (90/5) five-day capture histories, whereby individuals received a 1 if they visited a feeder during a given five-day interval and a 0 if they did not. The goal of this analysis was to determine whether survival varied as a function of an individual's metabolic phenotype. We modeled survival in two steps by first finding the model with greatest support that explained detection probability ( $p$ ), holding survival ( $\Phi$ ) constant and then finding the best model that explained the greatest variation in survival. We considered six models for detection including: holding  $p$  constant, allowing  $p$  to vary by fragmentation type, as a function of temperature, metabolic rate, or age, and lastly, as an interaction between temperature and fragmentation type. We used Akaike's information criteria adjusted for small sample sizes ( $AIC_c$ ) to select the best model (lowest  $AIC_c$ ) that explained variation in detection probabilities (Burnham and Anderson 2002). We considered models within  $2 \Delta AIC_c$  to be competitive (Burnham and Anderson 2002). Next, we included the model structure selected in the first step and ran models for survival probability ( $\Phi$ ). We considered five a priori models: constant survival,  $\Phi$  varies as a function of metabolic rate, or age, by fragmentation type and the interaction between metabolic rate and fragmentation type. We used  $AIC_c$  to select the top model corresponding to the lowest  $AIC_c$  value, and used this model to make inferences about survival and detection probability. We used the Delta method (Powell 2007) to estimate the 95% confidence intervals for overwinter survival probability. Lastly, we calculated  $\hat{c}$  as a measure of goodness-of-fit using 1000 parametric bootstraps implemented in Program MARK. The estimate of  $\hat{c}$  was then used to correct the precision of our parameter estimates for overdispersion.

## Data deposition

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.5620vc8> > (Latimer et al. 2018).

## Results

We obtained metabolic measurements on 27 chickadees; however, mechanical difficulties precluded the measurement of  $M_{SUM}$  on two birds. Due to the small sample sizes at each site, in subsequent analyses we pooled individuals from fragmented ( $N_{frag1} = 6$ ,  $N_{frag2} = 6$ ,  $N_{pooled} = 12$ ) and contiguous landscapes ( $N_{contiguous1} = 7$ ,  $N_{contiguous2} = 6$ ,  $N_{pooled} = 13$ ).

## Metabolic differences

Across fragmentation types, birds did not differ by weight at time of capture ( $t = 0.63$ ,  $df = 23$ ,  $p = 0.532$ ) or just prior to BMR trials ( $t = 0.29$ ,  $df = 23$ ,  $p = 0.582$ ), nor did they differ in body temperatures after BMR trials ( $t = 1.39$ ,  $df = 23$ ,  $p = 0.177$ ) or  $M_{SUM}$  trials ( $t = 0.976$ ,  $df = 23$ ,  $p = 0.339$ ). Age was not significantly related to BMR ( $t = -1.48$ ,  $df = 23$ ,  $p = 0.152$ ) or  $M_{SUM}$  ( $t = -1.55$ ,  $df = 23$ ,  $p = 0.136$ ). Measurements of BMR ( $t = 0.342$ ,  $df = 23$ ,  $p = 0.735$ ),  $M_{SUM}$  ( $t = 0.199$ ,  $df = 23$ ,  $p = 0.844$ ) or body mass ( $t = 0.082$ ,  $df = 23$ ,  $p = 0.935$ ) did not vary by capture date. However, the overall metabolic phenotype differed significantly between fragmented and contiguous forest habitats even after accounting for differences in average temperatures experienced 30 days prior to metabolic measurements. Birds in fragmented landscapes had an average of 8% lower BMR ( $t = 2.17$ ,  $df = 23$ ,  $p = 0.04$ ; Fig. 2) and 6% higher  $M_{SUM}$  ( $t = 1.65$ ,  $df = 23$ ,  $p = 0.12$ ; Fig. 2), resulting in a 10% higher AAS ( $M_{SUM} - BMR$ ) over birds in contiguous landscapes ( $t = 2.09$ ,  $df = 23$ ,  $p = 0.04$ ; Fig. 2). BMR showed a weakly positive but significant relationship with  $M_{SUM}$  ( $r = 0.45$ ,  $p = 0.04$ ).

## Variability in feeder visitation rates

We recorded 39 146 unique feeder visits from 25 individual chickadees over 90 days. Overall, birds increased their feeder visitation rates at lower temperatures ( $\beta = -0.132 \pm 0.03$ ,

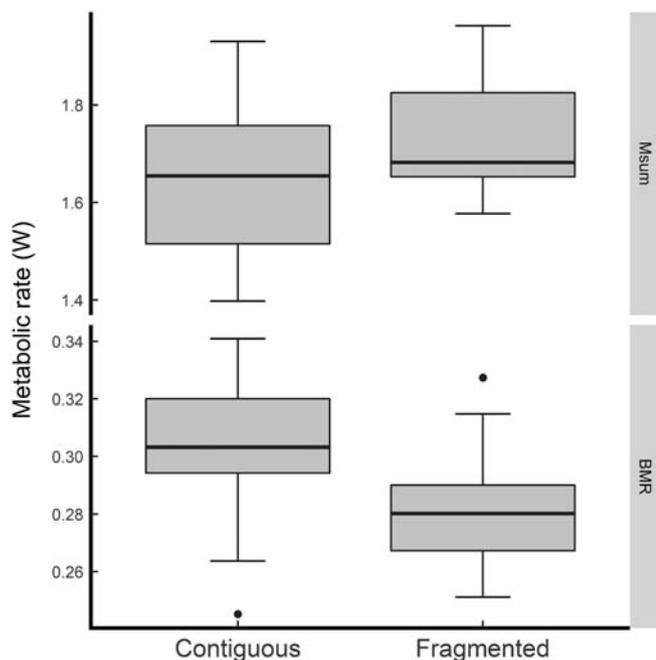


Figure 2. The population-level differences in basal metabolic rate (BMR; Watts), summit metabolic rate ( $M_{SUM}$ ; Watts) and absolute aerobic metabolic scope. Note, the actual vertical distance between the population averages for BMR and  $M_{SUM}$  reflect the average population difference between absolute aerobic scope (AAS), although the axes are plotted on separate scales for visual representation.

$p < 0.001$ ; Table 1, Fig. 3), and on snowier days ( $\beta = 0.06 \pm 0.02$ ,  $p = 0.011$ ; Table 1, but there was significant individual variation in feeder visitation in response to changes in ambient temperature (LRT:  $\chi^2 = 419.03$ ,  $p < 0.001$ ; Fig. 3, Supplementary material Appendix 1 Fig. A2). We found evidence that variation in feeder visitation as a function of ambient temperature could be explained by differences in  $M_{SUM}$  ( $\beta = 0.093 \pm 0.030$ ,  $p < 0.01$ ; Table 1), but not BMR ( $\beta = 0.004 \pm 0.028$ ,  $p = 0.893$ ; Table 1). Birds with lower  $M_{SUM}$  were more sensitive to changes in temperature and increased the rate at which they visited feeders over birds with higher  $M_{SUM}$  in response to decreases in ambient temperatures (Fig. 4). Although individuals with higher  $M_{SUM}$  visited feeders less overall throughout the winter ( $\beta = -0.399 \pm 0.202$ ,  $p < 0.05$ ; Table 1, Supplementary material Appendix 1 Fig. A1), we did not find evidence that average feeder visitation was influenced by BMR ( $\beta = -0.238 \pm 0.217$ ,  $p = 0.27$ ; Table 1, Supplementary material Appendix 1 Fig. A1).

At a population level, birds visited feeders at similar rates in fragmented and contiguous landscapes after controlling for differences in  $M_{SUM}$  ( $\beta = 0.269 \pm 0.59$ ,  $p = 0.64$ ; Table 1) and BMR ( $\beta = 0.046 \pm 0.46$ ,  $p = 0.92$ ; Table 1). In addition, the degree to which birds increased feeder visitation in response to decreasing temperatures was lower in fragmented landscapes after controlling for  $M_{SUM}$  ( $\beta = 0.155 \pm 0.05$ ,  $p < 0.01$ ; Table 1) and BMR ( $\beta = 0.221 \pm 0.05$ ,  $p < 0.001$ ; Table 1). Consequently, birds in fragmented landscapes visited feeders more-or-less consistently throughout winter regardless of temperature. In contrast, birds in contiguous landscapes increased their foraging activity at colder temperatures (Table 1, Fig. 3 - bolded lines, Supplementary material Appendix 1 Fig. A2). Not including woodlot as a random effect did not change the results except that  $M_{SUM}$  became only marginally significant; all other results remained unchanged (Supplementary material Appendix 1 Table A3).

## Overwinter survival

The top model for survival with  $M_{SUM}$  as a predictor received 66% of the model weight ( $w_i = 0.66$ ) and indicated that detection probability was relatively high ( $0.94 \pm 0.016$ ) and constant. Survival was similar between fragmented and contiguous landscapes, but increased with increasing levels of thermogenic capacity particularly in fragmented landscapes (Table 2, Fig. 5). Survival did not vary between young or old birds in our sample. The strong positive interaction between  $M_{SUM}$  and fragmentation type indicated that birds in contiguous landscapes had consistently high overwinter survival probabilities regardless of metabolic rates, but survival probability was positively related to  $M_{SUM}$  in fragmented landscapes (Table 3). Birds in fragmented landscapes with  $M_{SUM}$  below 1.65 W had winter survival probabilities below 50% (Fig. 5). As a result, a bird with an  $M_{SUM}$  of 1.65 W would have a 46% greater chance of surviving winter (80% versus 50%) in a contiguous landscape than in a fragmented one.

Table 1. Relationships between daily feeder visitation rates and predictors thought to influence the foraging intensity of free-living black-capped chickadees residing in forested sites in Dane County Wisconsin, USA. Results were obtained from generalized linear mixed-effects models with a Poisson error distribution. Fixed effects for  $M_{SUM}$  and BMR were modeled separately. Random effects included individual ID (nested within woodlot) to control for non-independence among individuals in each population. Fixed effects significant at the  $\alpha = 0.05$  level are indicated in bold. \* fragmented = 1, contiguous = 0.

| Fixed effects                       | $M_{SUM}$ model |             |             |                  | BMR model    |             |             |                  |
|-------------------------------------|-----------------|-------------|-------------|------------------|--------------|-------------|-------------|------------------|
|                                     | Beta            | SE          | z           | p                | Beta         | SE          | z           | p                |
| Intercept                           | <b>2.80</b>     | <b>0.41</b> | <b>6.79</b> | <b>&lt;0.001</b> | <b>2.86</b>  | <b>0.33</b> | <b>8.74</b> | <b>&lt;0.001</b> |
| $M_{SUM}$                           | <b>-0.40</b>    | <b>0.20</b> | <b>1.98</b> | <b>0.04</b>      | –            | –           | –           | –                |
| BMR                                 | –               | –           | –           | –                | -0.24        | 0.22        | 1.09        | 0.279            |
| Temperature                         | <b>-0.13</b>    | <b>0.03</b> | <b>3.53</b> | <b>&lt;0.001</b> | <b>-0.17</b> | <b>0.04</b> | <b>4.70</b> | <b>&lt;0.001</b> |
| Snow                                | <b>0.06</b>     | <b>0.02</b> | <b>2.52</b> | <b>0.011</b>     | <b>0.06</b>  | <b>0.02</b> | <b>2.49</b> | <b>0.013</b>     |
| Fragmentation*                      | 0.27            | 0.59        | 0.45        | 0.649            | 0.05         | 0.46        | 0.10        | 0.922            |
| Wing                                | -0.14           | 0.24        | 0.56        | 0.573            | 0.14         | 0.20        | 0.70        | 0.484            |
| $M_{SUM} \times$ Temperature        | <b>0.09</b>     | <b>0.03</b> | <b>3.05</b> | <b>&lt;0.005</b> | –            | –           | –           | –                |
| BMR $\times$ Temperature            | –               | –           | –           | –                | 0.003        | 0.03        | 0.13        | 0.893            |
| Temperature $\times$ Fragmentation* | <b>0.16</b>     | <b>0.06</b> | <b>2.64</b> | <b>0.008</b>     | <b>0.22</b>  | <b>0.05</b> | <b>4.04</b> | <b>&lt;0.001</b> |

| Random term         | $M_{SUM}$ |      |     | BMR      |      |     |
|---------------------|-----------|------|-----|----------|------|-----|
|                     | Variance  | SD   | n   | Variance | SD   | n   |
| Individual ID: Site | 0.73      | 0.85 | 22  | 0.91     | 0.76 | 22  |
| Site                | 0.20      | 0.45 | 4   | 0.04     | 0.21 | 4   |
| OLRE                | 0.58      | 0.76 | 974 | 0.59     | 0.77 | 974 |

In contrast, birds with  $M_{SUM}$  greater than 1.70 W would have similar overwinter survival probabilities (>80%) for contiguous and fragmented landscapes (Fig. 5). Model selection uncertainty was greater for models using BMR as a predictor, with three models having  $\Delta AIC_c$  values below 2 (Table 2). Nonetheless, the top model with BMR as a predictor received

50% of the model weight ( $w_i = 0.49$ ) and indicated that survival was constant and high ( $0.98 \pm 0.009$ ), and that birds with higher BMRs were more likely to be detected at feeders throughout the winter. Taken together, these results suggest that  $M_{SUM}$  is a more important determinant for overwinter survival than BMR.

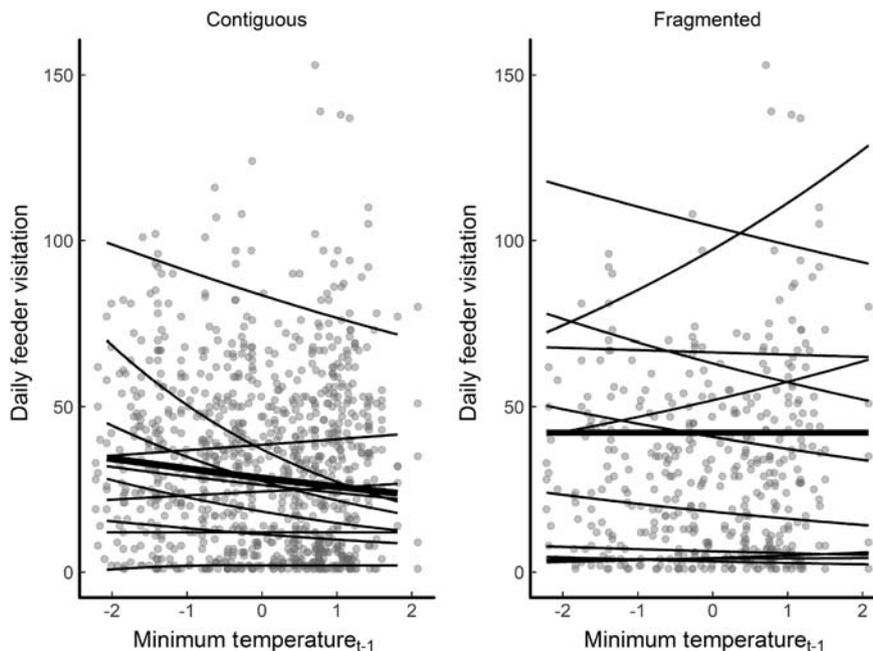


Figure 3. Predicted daily feeder visitation rate as a function of minimum daily temperature (centered and standardized) of the day prior for individual birds in fragmented and contiguous landscapes. Thin black lines show individual variation in daily feeder visitation, thick black line shows the population average. Raw data (no. visits/individual/day) are plotted as semi-transparent gray dots.

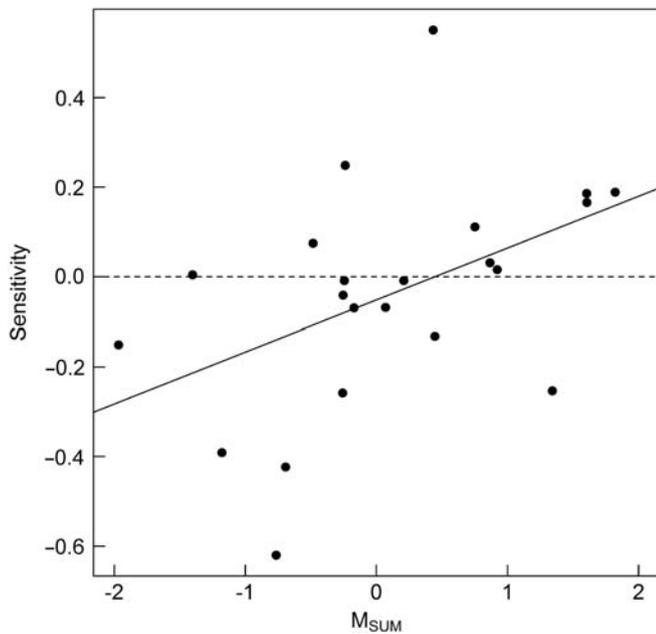


Figure 4. Sensitivity, as measured by the slope of the relationship between individual daily feeder visitation rate and minimum daily temperature of the day prior (from Fig. 3), plotted against an individuals' summit metabolic rate ( $M_{SUM}$ ; centered). Negative sensitivity values indicate birds that increased reliance on bird feeders as temperatures decreased throughout the winter, whereas positive values reflect birds that increased reliance on bird feeders as temperatures increased. In general, birds with low  $M_{SUM}$  were more sensitive (increased reliance on supplemental food) to changes in minimum temperatures throughout winter.

## Discussion

For many organisms, the ability to respond to environmental variability is mediated by complex relationships between physiology and behavior with potentially important implications on species demography (Kearney 2013). Here, we found evidence that individual differences in thermogenic capacity may contribute to differences in foraging patterns during a time of energetic stress with possible consequences for survival in human-modified landscapes.

Table 2. Model selection results for the probability of a black-capped chickadee surviving ( $\phi$ ) a given five-day interval during the winter season. Models are presented separately for  $M_{SUM}$  and BMR. We present models containing 80% of the model set weights. A (.) indicates an intercept only model; Frag was modeled as a categorical factor indicating whether an individual bird belonged to a population in a fragmented or contiguous forested landscape.

| Model                                  | K | AIC <sub>c</sub> | $\Delta$ AIC <sub>c</sub> | $w_i$ |
|--|---|------------------|---------------------------|-------|
| $M_{SUM}$                              |   |                  |                           |       |
| $\phi(M_{SUM} \times \text{Frag})p(.)$ | 4 | 145.46           | 0                         | 0.66  |
| $\phi(.)p(.)$                          | 2 | 148.72           | 3.30                      | 0.12  |
| BMR                                    |   |                  |                           |       |
| $\phi(.)p(\text{BMR})$                 | 3 | 148.04           | 0                         | 0.49  |
| $\phi(\text{Frag})p(\text{BMR})$       | 4 | 149.07           | 1.66                      | 0.21  |
| $\phi(\text{BMR})p(\text{BMR})$        | 4 | 149.94           | 1.89                      | 0.19  |

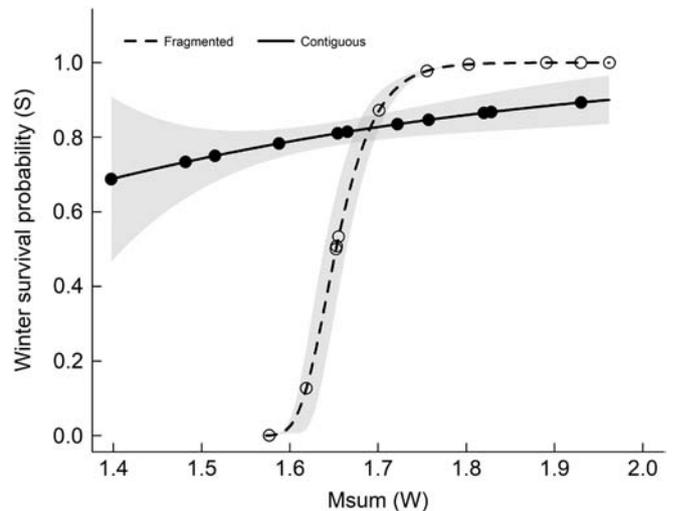


Figure 5. The relationship between overwinter survival probability ( $S$ ) and  $M_{SUM}$  (Watts) for birds in fragmented (dashed line) and contiguous forest sites (solid line). Gray shading indicates the 95% confidence intervals calculated using the Delta method. Filled and open circles represent predicted values for individuals captured in contiguous and fragmented landscapes, respectively.

In support of previous research, we found that bird foraging activity at feeders increased as winter temperatures decreased (Bonter et al. 2013), however, this relationship was mediated by individual differences in thermogenic capacity. Birds with low summit metabolic rates maintained greater levels of activity around feeders, and frequented them at higher rates as temperatures declined throughout winter. This finding appears to contradict previous research that suggests higher summit metabolic rates enable small endotherms to remain relatively more active under cold conditions (Sears et al. 2006). However, caution should be taken when comparing our results to previous studies as we only measured activity at supplemental feeding stations and cannot discount that birds with high summit metabolic rates may have been more active in the environment away from feeders. In particular, because chickadees cache food, individuals with high summit metabolic rates may have been more reliant on food caches away from supplemental feeding stations. We additionally found that birds increase their use of supplemental food on snowier days. This is consistent with previous findings that black-capped chickadee nutritional condition was lower during years with higher snow cover and suggests that snowfall can limit access to natural or cached food resources (Doherty and Grubb 2003). As bird feeders provide a stable, easily acquired resource, our results suggest that birds with low summit metabolic rates may rely more heavily on supplemental food to meet their energy demands, particularly during harsher winter weather.

Prior research suggests that birds increase foraging activities and reliance on supplemental food in fragmented landscapes due to differences in microclimates and food availability (Doherty and Grubb 2003). In our study, fragmented landscapes were 2°C colder on average, and experienced more

Table 3. Beta estimates, standard errors and lower, and upper 95% confidence limits for the mark–recapture model of the relationship between  $M_{SUM}$  and survival in contiguous and fragmented landscapes.  $\phi$  represents survival probability, and  $p$  represents capture probability.

| Parameter                        | B    | SE   | LCL   | UCL  |
|----------------------------------|------|------|-------|------|
| $\phi$                           |      |      |       |      |
| Intercept                        | 4.52 | 0.82 | 2.92  | 6.13 |
| $M_{SUM}$                        | 0.34 | 0.75 | -1.14 | 1.82 |
| $M_{SUM} \times \text{Fragment}$ | 4.66 | 1.83 | 1.06  | 8.26 |
| $p$                              |      |      |       |      |
| Intercept                        | 2.77 | 0.30 | 2.19  | 3.36 |

prolonged exposure (by 33%) to temperatures below  $-10^{\circ}\text{C}$  (Latimer and Zuckerberg 2017). Despite these conditions in fragmented forests, we did not find overall higher levels of foraging in fragmented landscapes. Instead, birds in fragmented forests exhibited relatively constant levels of feeder use throughout winter, regardless of temperature. This contrasts with the tendency for birds in contiguous landscapes to increase their use of supplemental food on colder days. This suggests that fragmented landscapes represent poorer quality habitats where individuals have to rely on feeders more or less consistently throughout the winter. Another possibility is that populations may differ in their level or use of heterothermy (Dammhahn et al. 2016). This controlled reduction in body temperature would reduce energy costs and foraging demands under colder conditions, and may partially explain why birds in fragmented landscapes foraged at slightly higher levels on warmer days. However, we lack data on relative use of heterothermy in the field. Alternatively, as predation risk generally increases with foraging activity (Lima 1986), birds may suppress feeding rates on cold days in order to balance the risk of predation with a reduction in body condition that occurs while foraging at high intensities (Houston and McNamara 2013). This may be particularly important in fragmented landscapes where the level or perception of predation risk may be greater (Crooks and Soulé 1999, Rodríguez et al. 2001). If fragmented landscapes are riskier (Crooks and Soulé 1999, Rodríguez et al. 2001), have harsher microclimates (Dolby and Grubb 1999, Latimer and Zuckerberg 2017), and fewer resources (Doherty and Grubb 2003), birds may adopt a predation risk-prone (higher intensity) foraging strategy on warmer days to minimize variance in long-term energy gains over the course of the winter and reduce their risk of starvation (Turcotte and Desrochers 2008). Our finding that birds in fragmented landscapes had significantly higher fat scores supports this idea and suggests that birds in fragmented landscapes may increase fat reserves as a strategy to help mitigate the consequences of greater uncertainty in energy gains (Mathot et al. 2012). In contiguous landscapes, where thermoregulatory demands are lower and resources higher (Doherty and Grubb 2003), birds may adopt a starvation risk-prone (lower intensity) foraging strategy on warmer days to minimize the risk of predation (Boysen et al. 2001). While we

did not explicitly measure food availability or predation risk, we found that birds in fragmented landscapes had approximately 8% lower basal metabolic costs than birds in contiguous landscapes. This pattern is consistent with other studies that have found reduced BMR in riskier (Mathot et al. 2016) and resource poor environments (Maldonado et al. 2012). Alternatively, the presence of feeders may have increased the densities of conspecifics, particularly in fragmented landscapes, which could have also led to an overall decrease in basal metabolic rates (DeLong et al. 2014).

The interaction between summit metabolic rate and behavioral responses to temperature can have several implications for overwinter survival in fragmented landscapes. Birds with higher summit metabolic rates were more likely to persist throughout winter especially in fragmented forests. One potential mechanism for this is that the high foraging intensity maintained by birds with low summit metabolic rates around feeders exposes them to greater risk of predation particularly at low temperatures (Lima 1986, McNamara et al. 1994). The advantages of having a high summit metabolic rate in fragmented landscapes may be twofold: first, because summit metabolic rate is linked to maximum thermogenic capacity, birds with higher summit metabolic rates may be better equipped to deal with colder temperatures often experienced in fragmented landscapes. Second, birds with higher summit metabolic rates may be less reliant on supplemental food resources, thereby reducing their exposure to predators. Only one other study has evaluated the relationship between thermogenic capacity and survival in wintering birds (Petit et al. 2016). Similar to their results, we found birds with higher summit metabolic rates benefited by having higher overwinter survival probabilities. However, we found this was only true for birds residing in fragmented landscapes. In our study, black-capped chickadees in fragmented forests needed to maintain 31% higher summit metabolic rates to achieve comparable survival rates as those in (Petit et al. 2016). This is possibly because our study was conducted during the second coldest winter (December through February; DJF) on record for Dane county, WI with an average winter temperature of  $3.24^{\circ}\text{C}$  below the 30-year average (Midwest Climate Center). Thus, the combination of warmer microclimates and available resources may have been sufficient to offset the negative impact of such a severe winter in contiguous landscapes, but not in highly fragmented ones (Doherty and Grubb 2003). One potential limitation of our study is that birds had constant access to supplemental food throughout winter, possibly leading to higher survival estimates than would be expected if food were restricted to specific days. However, Doherty and Grubb (2002) found that food-supplemented populations of Carolina chickadees in fragmented forests had lower survival probabilities than unsupplemented populations in contiguous forests, and that unsupplemented populations residing in fragmented forests had the lowest winter survival probabilities. Therefore, all else being equal, we expect our results would be even stronger had access to supplemental food been restricted to specific times throughout the winter.

Taken together, our results suggest that increased selection against birds with low summit metabolic rates in fragmented landscapes may be partly responsible for the differences in metabolic phenotypes we observed between fragmented and contiguous landscapes. Birds occupying fragmented forests had a 10% higher absolute aerobic scope ( $M_{\text{SUM}} - \text{BMR}$ ) over birds in contiguous forests. This suggests a greater capacity for birds in fragmented landscapes to elevate metabolic rates above basal levels for thermogenesis. Consequently, selection in human-modified environments may favor individuals that are able to simultaneously maintain a high thermogenic capacity with reduced maintenance costs. Interestingly, this complements a recent study that found geographic gradients in metabolic expansibility measured across multiple bird species were driven by increases in thermogenic capacity (Stager et al. 2015). Therefore, we suggest that greater metabolic expansibility may allow species to occupy colder climates across broad geographic gradients (Stager et al. 2015), but processes such as variability in food, microclimates, and predation risk become more important at local scales.

Winter is a critical time of year for many species and ecological processes (Williams et al. 2014), and habitat fragmentation will likely interact with climate change to further influence these processes (Opdam and Wascher 2004). We posit that fragmentation favors metabolic phenotypes with increased thermogenic capacity, reduced basal metabolic costs, and that are subsequently less sensitive to environmental variation and climate variability. Although the exact mechanism (predation, microclimate, resources) remains to be tested, we suggest that habitat fragmentation may select for climate-resilient phenotypes. This does not suggest, however, that the removal and fragmentation of habitats is a viable option to facilitate adaptation and resilience to climate change. Future studies should focus on underlying mechanisms that alter relationships between physiology and behavior and their fitness consequences across gradients of human modification.

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*Author contributions* – CEL, SJC and BZ conceived the ideas and designed the methodology; CEL and SJC collected the metabolic measurements with logistical support from WHK; CEL and BZ conceived and implemented the RFID data collection; CEL

analyzed the data with guidance from BZ; CEL and BZ led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supplementary material (available online as Appendix oik-05111 at <[www.oikosjournal.org/appendix/oik-05111](http://www.oikosjournal.org/appendix/oik-05111)>). Appendix 1.