Full Title: Age, sex, and temperature shape within- and among-individual space use in black-capped chickadees

Authors: Megan LaRocque[1,*], Jan J. Wijmenga[1], and Kimberley J. Mathot[1,2]

[1] Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9. Canada

[2] Canada Research Chair in Integrative Ecology

*Author for correspondence: mgfroese@ualberta.ca

Lay Summary

Feeding rates in black-capped chickadees increase with decreasing ambient temperature. Females, but not males, meet increased feeding rates by increasing the number of unique feeders visited, consistent with males, the dominant sex, having priority access to feeders. Across all temperatures, we observed age-related differences in number of feeders used in males, but not females. We suggest juvenile males may gain additional benefits, such as access to mates, from higher space used compared to adult males.

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Data availability statement: All data and R-code required to replicate the results have been submitted for review and will be archived on DRYAD upon acceptance of the manuscript.

Abstract

Historically, spatial ecology studies have focused on average movement patterns within animal groups; however, recent studies highlight the value of considering movement decisions both within- and among-individuals. Using a marked population of black-capped chickadees (*Poecile atricapillus*), we used the number of unique feeders an individual visits within our study area as a proxy for space use to assess the causes and consequences of within- and among-individual differences in chickadee space use. We found that as temperature decreased, feeding rate increased. Females, but not males, increased the number of unique feeders used coincident with the temperature-related increase in feeding rates. This may be due to sex-related differences in dominance, where males which are the dominant sex in chickadees, have priority access to feeders, while females increase their foraging areas to meet higher energetic demand. We also found that independent of temperature, juvenile males used more unique feeders than adult males. We suggest that this may be due to age-specific benefits of space use in male, where un-paired juvenile males may increase feeder exploration to gain information about potential mates. Finally, although chickadees showed repeatable differences in space use throughout our study, we found no evidence that space use predicted annual survival. Overall, our results suggest that dominance hierarchies and individual energetics impact within- and among-individual variation in space use. We provide suggestions for future studies to enhance understanding of fitness-related consequences of within- and among-individual variation in space use.

Keywords: spatial ecology, black-capped chickadees, spatial personality, foraging behavior, dominance hierarchies, *Poecile atricapillus*

Introduction

Spatial ecology is the study of population- or individual-level change in space use, and can be studied across varying spatial and/or temporal scales (Nathan, et al., 2008). Studies have shown that spatial behavior can be influenced by both external and internal factors. For example, timing of migration in several species of North American wood warblers (family Parulidae) has advanced over the last 5 decades with increasing spring temperatures (Horton, et al., 2023). At a finer spatiotemporal scale, diurnal movements of female elk (*Cervus elaphus*) are shaped by predation risk (Amor, et al., 2019), and several species of birds have been shown to decrease daily distances travelled when environmental conditions are more energetically challenging (e.g., high wind velocity or low ambient temperatures) (Grubb, 1978). Movement patterns are also influenced by intrinsic individual factors. For example, dominant red foxes (*Vulpes vulpes*) tend to visit more food patches on their territory while subordinates are competitively excluded, and therefore forced to visit food patches outside of their territory (Dorning and Harris, 2017), and female mule deer (*Odocoileus hemionus*) select gentle south-facing slopes prior to parturition, and steep north-facing slopes following parturition (Long, et al., 2009).

Historically, studies of spatial ecology have focused on mean patterns within populations or cohorts (also called mean-field approach; Morales, et al., 2010). However, with the advancement of passive movement-tracking technologies there is a growing trend to monitor and quantify within- and among-individual variation in spatial behaviors within populations simultaneously (Hertel, et al., 2020; Spiegel, et al., 2017). For example, there is evidence that individuals within a population will exhibit consistent differences in space use, termed “spatial personality” (Stuber, et al., 2022), and importantly, among- and within- individual differences in spatial behavior may interact such that among-individual differences in space use predict within-individual plasticity in space use. For example, individuals that have relatively higher space use on average are more likely to reduce space use as the density of territorial individuals in the population decreases (e.g., Lenda, et al., 2012; Newton and Rothery, 2001; Penteriani, et al., 2011; Robles and Ciudad, 2017). This is thought to reflect the transition from non-territoriality to territoriality when territory vacancies arise due to mortality of territorial individuals (Lenda, et al., 2012; Newton and Rothery, 2001; Penteriani, et al., 2011; Robles and Ciudad, 2017). Among-individual differences in dominance can also simultaneously influence within- and among-individual patterns of space use. For example, in a population of willow tits (*Parus montanus*), during mild winter temperatures, dominant adults forage in the innermost parts of trees more often than subordinate juveniles (Brotons, et al., 2000). Under colder temperatures, dominants can achieve their required intake while maintaining their positions in the innermost parts of trees, while subordinate juveniles are forced to increase their relative use of the outer parts of trees. This is consistent with numerous studies that have now shown that when a change in environmental conditions puts stress on a population, dominant individuals are able to maintain their spatial patterns and hold territory due to their competitive advantage over subordinates to control essential survival resources, while subordinates are forced to alter their patterns of space use (e.g., Desrochers, et al., 1988; Found and Clair, 2016; Hogstad, 2015; Matthews and Wong, 2015). Studies have not only aimed to investigate the causes of variation in space use (see above), but also to understand its consequences. For example, an individual that increases its space use may in turn increase its access to both food (Sells, et al., 2022) and social partners (Brown and Orians, 1970), benefitting its individual fitness. However, there is also evidence that individuals that use more space, have an increased risk of pathogen transmission (Barber and Dingemanse, 2010; Boyer, et al., 2010) and predation risk (Lima and Dill, 1990).

Avian systems are excellent models for studying spatial ecology because they exhibit a diversity of spatial behaviors, including migration (e.g., Bruderer, et al., 2018), territoriality (e.g., Campioni, et al., 2013), and floating (i.e., non-territoriality; e.g., Smith, 1984). The spatial behavior of small non-migratory birds is particularly interesting from an energy management perspective because the winter months can be challenging due to shortened daylength and low natural food availability combined with increased costs of thermoregulation (Cooper, 2000; Studd, et al., 2021; Sutton, et al., 2021). Individual movement both consumes energy reserves and produces metabolic heat (Cooper and Sonsthagen, 2007; Humphries and Careau, 2011). Not surprisingly, wintering birds adjust their movement choices based on environmental changes as well as changes in habitat gaps and boundaries (Bailey, et al., 2018; Desrochers and Fortin, 2000; Turcotte and Desrochers, 2005), food availability (Brotons and Herrando, 2003; Mady, et al., 2021; Smith and Van Buskirk, 1988), season (e.g., breeding versus non-breeding) (Brittingham and Temple, 1992; Lemmon, et al., 1997), and temperature (Alatalo, 1982; Hogstad, 2015). Given the increased energetic costs of maintaining homeostasis for small over-wintering birds, decreasing winter temperature may have important implications for individual movement decisions related to gathering food. If birds have a fixed energy budget, increased costs of thermoregulation during the cold would require reduced energy expenditure on activity (Cooper, 2000; Grubb, 1978). Alternatively, if birds can modify their total energy budget (Cooper and Sonsthagen, 2007), or allocate heat generated via activity towards thermoregulation (Humphries and Careau, 2011), then higher costs of thermoregulation may be met by increasing foraging activity (e.g., Bonter, et al., 2013; Kessel, 1976; Latimer, et al., 2018). Among-individual differences in spatial behavior have also been found to relate to individual state variables relating to dominance rank. For example, in some avian species older birds (Brotons, et al., 2000) as well as males (Hogstad, 2015) presumably monopolize resources, allowing them to restrict their space use to smaller, safer areas. Therefore, analyzing possible correlates of both within- and among-individual differences in space use of small, resident winter birds may provide insight into the predictors of individual resident bird survival throughout the winter months.

Our study used a marked population of black-capped chickadees (*Poecile atricapillus*; henceforth referred to as 'chickadees') to address questions related to both within- (i.e., plasticity), and among- (i.e., personality) individual differences in space use. Specifically, we asked: 1) how is within-individual variation in space use influenced by ambient temperature; 2) do individuals show repeatable variation in space use (i.e., spatial personality); 3) are among-individual differences in space use predicted by individual state variables related to dominance (sex and age); 4) do dominance-related state variables predict the spatial behavior response of individuals to temperature change; and 5) are among-individual differences in space use associated with differences in annual survival. If the number of unique feeders visited corresponds with individual activity level, then we predict that individuals may either reduce the number of unique feeders used during colder ambient temperatures to conserve energy or increase the number of unique feeders used during colder ambient temperatures to increase access to food. If among-individual differences in space use are present, we predict that dominant individuals would use a lower number of unique feeders compared with subordinates given their ability to monopolize food resources. Furthermore, we predict that as temperature decreases subordinate individuals will have a steeper reaction norm (i.e., greater change in their space use, either positive or negative) compared to dominants. We used age and sex as proxies for dominance rank as males are dominant to females and, within sex, older birds are dominant over younger birds in black-capped chickadees (Smith, 1997). We also analyzed within- and among-individual differences in feeding rates to evaluate the role of food acquisition in shaping space use decisions at both the within- and among-individual levels. Finally, we investigated whether among-individual differences in space use were associated with differences in annual survival. We did not have strong a priori predictions for this association since our predictions depend on the results of dominance effects. Our results expand understanding of the mechanisms underlying within- and among-individual variation in space use and discuss potential fitness consequences of space use variation during the winter season in a non-migratory passerine.

Methods

Study site and study population

This study was conducted between October 2022 and March 2023 in a marked population of black-capped chickadees at the University of Alberta Botanic Garden (UABG) in Devon, Alberta, Canada (53°2402700 N, 113°4504100 W). The UABG is located 22 km SW of Edmonton and 6 km N of Devon within the Devon Dunes natural area. It is a 0.97 km^2 property with 0.32 km^2 of display gardens and 0.65 km^2 of mixed wood forest. The marked population was established in October 2017, and standardized catching effort is done each fall (generally between October and December) to mark new birds. Birds are caught using mist-nets set up near 8 feeder locations spread throughout the 0.65 km^2 study area (see Supplementary Figure S1). Capture effort for the study year occurred between November 12, 2022, and January 2, 2023 (inclusive). Temperature data used in this study was obtained from the Edmonton International Airport (YEG) weather station, located 10 km SE of the study site (data provided by Alberta Agriculture and Forestry, ACIS: https://agriculture.alberta.ca/acis).

Upon initial capture, birds are fitted with a unique metal band provided by the Canadian Wildlife Service, and a unique combination of color bands, including leg bands embedded with passive integrated transponder (PIT) tags. A small blood sample is collected to allow for molecular sexing (Griffiths, et al., 1998). For birds without molecular sex data, we use a discriminant function to assign a highly probable sex (Sridharan, 2021) (see Supplementary Text S1). After birds are captured (whether initially or upon recapture), standard morphometric data are collected (body mass, wing length, bill length and depth, tarsus length), and the age of the bird is estimated using plumage characteristics. During fall catching, birds can be scored as hatch year or after hatch year. The birds present in our study ranged in minimum age from 0 years (i.e., hatched in spring 2022) to 6 years (i.e., hatched in spring 2016 or earlier).

Ethical note

This study was conducted in accordance with the University of Alberta Biosciences Animal Care and Use Committee (AUP00002210), the Alberta Wildlife Research Permit (#56631) and Collection License (#56632) and Environmental Canada Canadian Wildlife Service (banding permits #10936 and 10936A). To minimize stress during capture, we did not attempt catching during inclement weather, and mist nets were monitored continuously to ensure birds were removed from the nets and processed quickly. Any birds that appeared stressed or unwell, were release immediately without being processed. For birds that were processed, morphometric measurements, banding, and blood sampling was completed in under 10 min before birds were released at the site of capture. For molecular sexing, a small (<20μl) blood sample was collected from the brachial vein of initially captured birds (i.e., only one blood sample was collected for each bird).

Spatial use data

Each feeder is equipped with an RFID antenna that automatically records the date, time, and unique transponder hex code of each PIT tagged individual whenever it visits a feeder. Although RFID equipped feeders filled with black-oil sunflower seeds were present in the study area between October 29th, 2022 to February 28th, 2023 (inclusive), we used only a subset of the data for our analyses of spatial behavior. First, we restricted the data set based on dates and included only feeder visit data collected between January 9th and February 14th, 2023. We used January 9th, 2023 (one week post catching) as the start date to reduce the effect that catching efforts may have on spatial behavior (e.g., displacing individuals from feeders where catching was occurring). Between February 15th and February 23rd, 2023 (inclusive), one of the 8 feeders had a damaged circuit board resulting in complete loss of data during that time interval, and thus we removed this 8-day period from our data analysis. Although we did collect an additional 5 days of data at feeders from February 24th to 28th, 2023 (inclusive), we chose not to include these dates in our analyses due to 1) the large temporal break in otherwise continuous data, and 2) because this break coincided with a time where the spatial dynamics of chickadee flocks were likely changing. Chickadees can begin to establish breeding territories in early February which can initiate winter flock break up (Smith, 1992). However, we present results in Supplementary Table S1 that include feeder data collected from February 24th to 28th for full transparency (see Supplementary Text S2 for details).

Second, we restricted which birds were included in the dataset based on their use of the “thermal feeder”. In the study year, one of 8 regular feeder locations within the study area was equipped with a different frequency RFID system as part of another study aimed at understanding variation in body temperature in chickadees (referred to as “thermal feeder”). This system was installed from December 4th, 2022, to March 17th, 2023, and required a different type of PIT tag and RFID antenna frequency, which meant that the majority of birds in the marked population could not be detected at the thermal feeder during the relevant dates for the present study. We relied on the feeder visits recorded between October 29th and December 4th, 2022 (inclusive), across all feeders to filter out birds that were known to have used the thermal feeder location from our study sample (N=32). Furthermore, we removed N=1 individual that was initially identified (i.e., tagged and given a unique ID) at this feeder after December 4th. Although we cannot exclude the possibility that remaining birds in our dataset commenced using the thermal feeder after December 4th, if they did, this would mean that our estimates of within- and among-individual variation are underestimated, and thus make our results conservative.

Finally, we removed individuals (N=3) for which we did not have molecular sex data and additionally whose sex assignment using the discriminant function was inconclusive (See Supplementary Text S1 and Sridharan, 2021). This resulted in a total of 138 uniquely identified (i.e., PIT-tagged) individuals for which we analyzed foraging activity at the 7 remaining feeders.

We analyzed space use at the level of days by summing the total number of unique feeders visited by each individual during each of the 37 study days from January 9th to February 14th, 2023 (inclusive). Neighbouring feeders are at least 270 m apart, corresponding to published estimates of chickadee winter territory size (Smith, 1992; see Supplementary Figure S1). We used the number of unique feeders visited by an individual as a proxy for an individual's space use. Since this proxy is coarse due to the small number of sampling points (i.e., feeders), we were prevented from using more refined approaches to estimate space use. Not being able to use minimum convex polygons, local convex hull, or kernel density estimation for instance, decreases our precision, and therefore power to detect statistically significant associations. Thus, our conclusions regarding the relationships of sex, age, and temperature with patterns of space use are likely conservative. We also summed the total number of feeder visits made by each individual during each of the 37 days to allow us to assess daily feeding rate. For individuals that were not detected at any feeders within a day, we assigned them a unique feeder count and visit count of ‘0’. If an individual was never detected at any of the feeders in any subsequent days after a unique feeder count and visit count of ‘0’ (i.e., it had a unique feeder count and visit count of ‘0’ from the initial ‘0’ entry until February 14th, 2023), we assumed that the individual may have died, and we replaced the sequence of ‘0s’ with ‘NAs’. This occurred for a total of N=5 individuals.

Data analysis

All statistical analyses were conducted in the R-statistical environment v. 4.0.3 (R Development Core Team, 2020) using the R-studio interface (R Studio Team, 2020). We constructed two separate linear mixed-effects models (LMMs) to explore sources of variation in total number of feeders used and total daily feeding rate. Models were fitted with Gaussian error distributions using the “lmer” function in the “lme4” package (Bates, et al., 2015). We verified that model residuals were normally distributed by visual inspection, which they were. Temperature was standardized prior to analyses by dividing values by 2 standard deviations (s.d.) so that the estimated effect of temperature reflects the effect of 1 s.d. change in temperature (i.e., 5.74°C), facilitating comparison with Age-Sex effects sizes (Gelman, 2008). Given that most birds were minimum age 0 or 1 (Age 0: N =70, Age 1: N = 37, Age 2: N = 18, Age 3: N = 3, Age 4: N = 5, Age 5: N = 3, Age 6: N = 2), we binned age into two categories for analysis: AgeBin = 0, birds hatched in 2022, “juveniles”; AgeBin = 1, birds hatched in 2021 or earlier, “adults”. Both models included fixed effects of standardized temperature and “Age-Sex”. “Age-Sex” was a composite variable specifying the age (0 = juvenile or 1 = adult) and sex (male or female) of each individual, resulting in four levels (juvenile male, juvenile female, adult male, adult female). We also included the interaction between Age-Sex and standardized temperature to account for possible interacting effects of dominance on response to temperature change. Finally, we included individual ID (i.e., transponder hex code) as a random effect in both LMMs to account for non-independence of repeated measures data on the same individuals, and to assess among-individual variation and repeatability of unique feeder counts and feeding rates. Adjusted repeatabilities for both responses were estimated using the ‘rptR’ package (Stoffel, et al., 2017).

Given that we observed repeatable among-individual differences in both space use and feeding rates (see Results), we also wanted to evaluate whether these among-individual differences were associated with differences in annual survival. To do this, we obtained RFID detection data for the birds included in our study in the next fall (September 10, 2023, through October 21, 2023). Because chickadees are non-migratory and form winter flocks that are stable across years, birds that were not detected the following autumn were assumed to have died rather than emigrated and were assigned a survival value of 0 (N = 58). Birds that were detected were confirmed to have survived and were assigned a survival value of 1 (N = 80). Initially, we tried to estimate the among-individual correlation between space use and feeding rate using two bivariate models, however, we were unable to achieve good model convergence across numerous prior specifications. Thus, we instead ran univariate generalized linear models (GLMs) of survival (yes/no) as a function of the best linear unbiased predictors (BLUPs) of a bivariate model including both unique feeder count and visit count as responses, and the fixed and random effects as in the LMMs described above. To account for BLUP uncertainty, we ran each GLM of survival 1000 times using an estimate drawn from the distribution of BLUPs for unique feeder count and visit count (Hadfield, et al., 2010). The 1000 estimated effects sizes of unique feeder count and visit count on survival were used to derive an estimated effect size and 95% CI for the relationship between unique feeder count or visit count on annual survival. All GLMs with survival as a fixed effect were fitted with a binomial error distribution. See also Haave-Audet, et al. (2024) for further justification and description of this approach.

We obtained the fixed effect mode and 95% confidence intervals (CIs) of the posterior distribution of 1000 simulations of the LMMs using the 'sim' function of the 'arm' package (Gelman and Su, 2015). We used the 95% CI to evaluate the level of support for a given effect. 95% CIs that did not overlap zero were described as providing strong support for an effect, while estimates that were centered on zero were described as providing strong support for lack of an effect, or no support for an effect. For estimates not centred on zero but whose 95% CI overlapped zero, we calculated the proportion of estimates that were above (for negative mean estimates) or below (for positive mean estimates) zero (i.e., Bayesian p-values), to aid in the interpretation of the strength of support. We interpreted estimates biased away from zero but whose CIs had up to 15% overlap with zero (i.e., p = 0.15) as providing moderate support for an effect because this corresponds to five times greater support (i.e., 0.75/0.15) for the interpretation of an effect in the reported direction compared to the interpretation of an effect in the opposing direction (Marsman & Wagenmakers, 2017).

Results

Since our predictions on spatial patterns were contingent on whether chickadees adjust their total energy expenditure in response to temperature and/or differ in energy expenditure, we first looked at the effect of temperature, sex, and age on feeding rate (Table 1). We found that under relatively mild winter condition (at 0°C), juvenile males (β = 63.20, 95% CI = 55.62, 75.05) and adult males (β = 65.70, 95% CI = 59.07, 75.65) made more visits to feeders than juvenile females (β = 59.10, 95% CI = 47.72, 64.16) and adult females (β = 57.73, 95% CI = 50.82, 67.37). We also found that all age and sex groups showed a significant change in the number of daily visits they made as a function of temperature (juvenile females: β = -15.93, 95% CI = -18.39, -12.54; juvenile males: β = -22.44, 95% CI = -25.78, -19.59; adult females: β = -9.67, 95% CI = -13.33, -7.03; adult males: β = -17.99, 95% CI = -21.54, -15.21), such that each Age-Sex group increased their feeder visits under colder conditions (Figure 1b). Finally, we found the number of feeder visits to be highly repeatable in our population (r = 0.54, 95% CI = 0.48, 0.60).

On average, individuals visited 1.2 out of the 7 possible feeders during any day (s.d. = 0.46, range: 0-5) and individuals were detected in 36.01 out of 37 possible days (s.d. = 4.60, range: 2-37). Throughout the study period, N=70 individuals visited exclusively 1 feeder, while the other N=68 individuals visited more than 1 feeder. We also observed sex and temperature related effects, with additional effects of age, on the number of unique feeders visited (Table 1). Under relatively mild winter condition (at 0^{o}C), juvenile males visited the greatest number of unique feeders (β = 1.25, 95% CI = 1.15, 1.37), while adult males visited the fewest unique feeders (β = 1.10, 95% CI = 1.00, 1.21). This difference was significant (contrast, β = 0.18, 95% CI = 0.00, 0.29, p = 0.03). Females visited an intermediate number of feeders but did not exhibit age-related differences in the number of unique feeders visited (juvenile: β = 1.16, 95% CI = 1.09, 1.28; adult: β = 1.17, 95% CI = 1.05, 1.27). We also found that response to temperature varied as a function of sex, but not age (Figure 1a). Specifically, changes in the number of feeders visited by male chickadees as a function of temperature did not differ from zero for either juvenile (β = -0.01, 95% CI = -0.06, 0.04) or adult birds (-0.005, 95% CI = -0.05, 0.04), but females showed significant changes in the number of unique feeders visited as a function of temperature (juvenile: β = -0.05, 95% CI = -0.10, -0.01;

adult: β = -0.05, 95% CI = -0.11, -0.01), such that they visited relatively more unique feeders under colder conditions. Finally, we found the number of unique feeders visited to be highly repeatable in our population (r = 0.44, 95% CI = 0.38, 0.50).

Out of N=138 individuals, N=80 birds were detected at feeders in the following Fall 2023 (57.97% survival rate). We found no support for an effect of unique feeder count on survival (β = -0.11, 95% CI = -0.32, 0.15). However, we found strong support for a positive effect of visit count on survival (β = 0.004, 95% CI = 0.002, 0.008).

Discussion

We studied patterns of spatial behavior and feeding rates in black-capped chickadees across a greater than 20°C temperature range (min: -17.1°C; max 4.7°C). We hypothesized two different mechanisms by which chickadees might cope with increasing energetic costs of thermoregulation with decreasing ambient temperatures in winter. First, if chickadees can increase their total energy expenditure under increased costs of thermoregulation, we predicted they would increase activity and movement behavior as a means of securing more resources (i.e., increasing feeding rate). Alternatively, if total energy expenditure is fixed, we predicted no change in feeding rates, and therefore that increased costs of thermoregulation would come at the cost of other activities (such as spatial movement). All chickadees, regardless of age or sex, increased feeding rate with decreasing ambient temperatures, consistent with the notion that chickadees increase total energy expenditure to meet the higher costs of thermoregulation. However, males, which are dominant over females (Smith, 1992), achieved this without changing patterns of space use, while subordinate females increased the number of unique feeders used with decreasing ambient temperatures. Taken together, our results suggest that dominance hierarchies based on sex and age as well as individual energetics play a role in shaping both among- and within-individual variation in space use as a function of temperature change in our population. Interestingly, we also observed age effects on spatial behavior in male, but not female chickadees, with juvenile males having a higher space use compared to adult males. Females, regardless of age, had intermediate space use compared to adult and juvenile males. This result cannot be explained by age and sex related dominance hierarchies in chickadees, as juvenile males are dominant over females (Smith, 1992). We suggest that patterns of space use in males may also be shaped by age-specific differences in access to breeding partners and discuss how future studies might test this.

We found that males have a higher feeding rate than females, regardless of age. This result is in line with other studies that found sex, but not age, effects on feeding rate in chickadees (Brittingham and Temple, 1992; Wilson, 2001). Our finding that males have a higher feeding rate than females may be because males are dominant over females (Smith, 1992), allowing them to monopolize feeders to achieve higher feeding rates (Ficken, et al., 1990). Additionally, because males are structurally larger than females, they have higher total metabolic rates compared with females (Desrochers, 1989; Lewden, et al., 2012; Ramsay and Ratcliffe, 2003), and therefore require more food intake to meet energy demands. However, we found no evidence of sex-related differences in the effect of temperature on feeding rates. As temperatures decreased, and therefore costs of thermoregulation increased, all chickadees increased feeding rates in a similar fashion, regardless of age/sex (Figure 1b). This is consistent with other studies that have assessed the effects of temperature on over-winter feeder use in chickadees (Bonter, et al., 2013; Latimer, et al., 2018). While the sex-specific patterns of feeding rate were consistent with dominance and/or whole-body metabolic rate shaping feeding rate in this study, we have observed variable sex-specific patterns in feeding rate in our study population across years and studies. While in most cases, males have been shown to have higher feeding rates than females (Arteaga-Torres, et al., 2020; Sridharan, 2021), we have also observed males to have lower feeding rates than females in one study year (although food was not offered continuously; Haave Audet, 2021), with no overall sex-related differences in feeding rate across four previous study years (LaRocque, et al., 2023). However, each of these studies compared feeding rates between males and females within a specific feeder location, not the sum of feeder visits across all feeder sites, and thus are not directly comparable to the current study. More work is required to understand which year-specific factors shape sex-specific feeding rates in chickadees.

Given that chickadees increase their food intake to meet increased costs of thermoregulation, we were interested in understanding how this would affect patterns of space use. Specifically, we predicted that dominant birds (males) would have priority access to feeders and would therefore be able to increase feeding rates without increasing space use, while subordinates (females) would require a higher space use to meet their higher energy demands. As predicted, as temperature decreased, males maintained their unique feeder count, while females used more unique feeders (Figure 1a). This is consistent with previous work that found that male chickadees tend to have priority access to feeders and are able to competitively exclude subordinate individuals from these food resources (Ficken, et al., 1990). However, we also found that juvenile males used more unique feeders compared with adult males, regardless of temperature, with females of both ages using an intermediate number of feeders (Figure 1a). This cannot be explained by dominance hierarchies alone, as juvenile males are dominant to females in chickadees (Smith, 1992). We suggest that age-related differences in space use in males may reflect age-specific differences in the benefits of spatial exploration. Previous work on chickadees has shown that non-territorial individuals (i.e., “floaters”) tend to be juveniles (Smith, 1984). Although we did not find evidence for age-related differences in space use of females in our study, we suggest that the higher space-use observed in juvenile males may reflect a floater strategy to increase their access to available females. Specifically, juvenile males in our population are more likely to be un-paired compared to adult males by definition because they have no prior breeding experience. As such, juvenile males may have a higher tendency to ‘float’ between flocks, searching for opportunities to insert into higher ranking mate-pairs (Smith, 1984). This suggests that rather than taking advantage of priority access to feeders, juvenile males may increase their unique feeder count to increase their access to future mates and/or insert themselves into widowed mate-pairs. This explanation is consistent with results from an earlier study that found that subordinate male mountain chickadees (*Poecile gambeli*) explore more than dominant males (Fox, et al., 2009). Furthermore, Benedict, et al. (2021) found that as mountain chickadees age, individuals reduce the number of unique feeders they visit, suggesting that as individuals age they gain experience and information that allows them to reduce resource exploration effort (Dall, et al., 2005; McNamara, et al., 2006). Future studies could address this age-specific space use by assessing whether juvenile males that have a higher space use in the winter also have higher success in finding a mate the following spring. We would also expect that if the population’s sex ratio became skewed towards a lower percentage of females than males, then juvenile males would increase their space use in an attempt to find a mate.

Since we found that unique feeder count was highly repeatable among individuals, even after considering individual sex and age differences, we predicted that among-individual variation in fitness consequences may exist. We found no evidence that the number of unique feeders visited by an individual predicts their annual survival. However, the more feeder visits an individual makes (i.e., higher feeding rate), the more likely they are to survive to the next fall. These results can be understood after considering the possibility that the extent to which an individual uses its territory may impact multiple facets of individual fitness. Although an increase in space use may increase an individuals' access to food (Sells, et al., 2022) and social partners (Brown and Orians, 1970), it may also increase pathogen transmission (Barber and Dingemanse, 2010; Boyer, et al., 2010) and predation vulnerability (Lima and Dill, 1990). Space use in our population may have combined positive and negative fitness correlates that do not necessarily vary predictably among individuals, providing support for our finding that among-individual differences in space use do not predict among-individual differences in annual survival.

Another possibility is that the relationship between space use and survival differs as a function of sex and/or age. Unfortunately, our sample sizes precluded us from assessing this meaningfully (see Figure S3 for sample sizes). However, in chickadees, males generally have higher survival compared with females (e.g., Haave-Audet, et al., 2024; Mathot, et al., 2022), presumably because their dominant status gives them priority access to food thereby decreasing their risk of starvation relative to females (Ficken, et al., 1990). Thus, the lack of effect of space use on survival may be due to the fact that males have both the highest (juveniles) and lowest (adults) space use. To evaluate whether sex-related differences in survival might obscure our ability to detect overall effects of space use, we conducted a post-hoc analysis on our current study's individuals to test for sex-related differences in survival (see Supplementary Text S3 for details). Contrary to our expectation, we found that males were less likely to survive to the next fall (log odds ratio = 0.15, CI = -0.33, 0.62) compared to females (log odds ratio = 0.50, CI = 0.02, 1.00) (also see Supplementary Figure S3). This is opposite to the sex-related differences in survival reported in two other study years in the same population (Haave-Audet, et al., 2024; Mathot, et al., 2022). However, in the present study chickadees were provided with continuous access to supplemental food (sunflower seeds) for the entire winter season, while in the previous studies, supplemental food was provided intermittently (Haave-Audet, et al., 2024), or birds experienced repeated foraging interruptions due to experimental manipulations of predation (Arteaga-Torres, et al., 2020; Mathot, et al., 2022). We suggest that providing continuous ad libitum food throughout the winter without imposing foraging interruptions may have negated the survival benefit male chickadees normally achieve through priority access to food (Ficken, et al., 1990). However, while several studies have reported sex-specific effects of food supplementation on survival in small passerines, these effects have been variable with dominant males sometimes benefitting most from supplemental food (Lahti, et al., 1998), and other times benefitting least (Krama, et al., 2023). Thus, the precise mechanism underlying the higher female survival observed in the current study is unclear and warrants further investigation.

As passive movement-tracking technologies advance, it is important to consider the impact of within- and among-individual variation as well as their interaction, on individual and population movement decisions. Taken together, our results are consistent with literature on chickadee over-winter feeder dominance where males tend to monopolize food resources and have priority access to food resources. However, we found evidence that adult males had the lowest unique feeder count, females had an intermediate count (regardless of age), and juvenile males had the highest, which suggests that additional factors are at play in shaping age- and sex-specific spatial patterns of feeder use. We suggest that space use by juvenile males may be shaped not only by priority access to food (allowing them to increase intake rates without increasing feeder use), but additionally by opportunities to encounter un-pair bonded females (favouring a higher number of unique feeders in juveniles compared to adult males). To assess this alternative benefit of increased space use in juvenile males, future work should assess whether differences in juvenile male winter space use predict spring mate success. If males use increased space use as a means of increasing encounter rates with available females, then we would also predict that decreased female abundance (either natural or experimental) would result in increase space use in juvenile males. Although we did not find any evidence that differences in space use were associated with differences in survival, it is possible that the sex-related differences in survival obscured space use effects that were independent of sex. Additionally, our measure of space use may have been too coarse to quantify such effects. Future studies would benefit from having a grid with more sampling points (i.e., feeders) to enable the use of more refined approaches to assess space use (e.g., minimum convex polygons or maximum kernel density; Socias-Martínez, et al., 2023). We also suggest that future studies assess the impacts of space use on characteristics such as reproductive status, and within Age-Sex dominance interactions to increase our understanding of the consequences of within- and among-individual differences in space use for resident winter birds.

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Figure legends

Figure 1. Predictions from the models for (a) the unique feeder count and (b) the feeding rate, in response to the average daily temperature under different ages (juvenile, adult) and sexes (female, male). In both panels, the lines represent the regression of different ages and sexes as a function of temperature. The grey regions represent 95% CIs. (Online version in color.)

Tables and table legends

Table 1. LMM model results for unique feeder count and feeding rate.

	Unique Feeder Count (number of unique feeders visited per day)	Feeding Rate (total number of feeder visits per day)
Fixed effects	*β (95% CI)*	*β (95% CI)*
Female – Juvenile[1]	1.16 (1.09, 1.28)	59.10 (47.72, 64.16)
Female – Adult	1.17 (1.05, 1.27)	57.73 (50.82, 67.37)
Male – Juvenile	1.25 (1.15, 1.37)	63.20 (55.62, 73.05)
Male – Adult	1.10 (1.00, 1.21)	65.70 (59.07, 75.65)
Female – Juvenile : Temperature	-0.05 (-0.10, -0.01)	-15.93 (-18.39, -12.54)
Female – Adult : Temperature	-0.05 (-0.11, -0.01)	-9.67 (-13.33, -7.03)
Male – Juvenile : Temperature	-0.01 (-0.06, 0.04)	-22.44 (-25.78, -19.59)
Male – Adult : Temperature	-0.005 (-0.05, 0.04)	-17.99 (-21.54, -15.21)
Random Effects	*σ (95% CI)*	*σ (95% CI)*
Transponder Hex Code N=138	0.09 (0.09, 0.10)	610.20 (573.35, 648.16)
Residual N= 4990	0.12 (0.11, 0.12)	516.41 (496.03, 537.22)
Repeatability	*r (95% CI)*	*r (95% CI)*
Transponder Hex Code N=138	0.44 (0.38, 0.50)	0.54 (0.48, 0.60)

Note, intercept values for Age-Sex categories are estimated at 0°C, and temperature was standardized prior to analysis, therefore estimate effect sizes are for 1 s.d. change in temperature (i.e., 5.74°C).

Figures

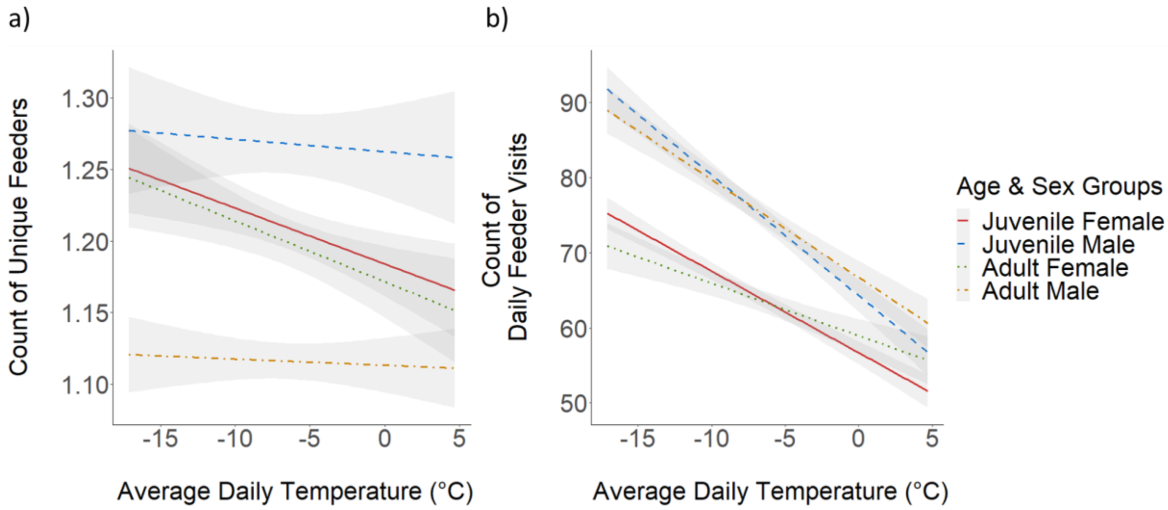

Figure 1.

Supplementary Materials for: Age, sex, and temperature shape within- and among-individual space use in black-capped chickadees

Authors: Redacted for review

Contents

Supplementary Text S1. Discriminant function for chickadee sex assignment**.**

For individuals in our dataset without molecular sex data (N=13), we used a discriminant function developed by Sridharan (2021) to assign a sex, when possible. This discriminant function was designed specifically for our population of black-capped chickadees based on a sample of 469 birds (238 females and 231 males). The discriminant function incorporates highly repeatable morphological traits (i.e., body mass, wing length, and tarsus length) as outlined in the following equation:

LD2 = 0.55886 (Body mass) + 1.0064 (Wing length) + 0.28042 (Tarsus length).

For those individuals who we had repeated morphological measures, we calculated the average of each trait measurement. Birds can conclusively be assigned ‘male’ if the discriminant function score is >81 and ‘female’ if the score is <77. Individuals who have scores that fall in the intermediate range ($78 \leq 81$) cannot be conclusively assigned as male or female. However, scores at the lower end of this range are more likely to be female (only 4% of individuals with scores of 77-78 were male) while scores at the higher end are more likely to be male (68% of individuals with scores of 80-81 were male). When we used the discriminant function, we removed individuals who did not have conclusive sex assignment (N=3). Therefore, the remaining individuals (N=10) could be assigned either ‘male’ or ‘female’ with 100% accuracy.

Supplementary Text S2. Analyses with versus without data from February 15th through 28th, 2023

Analyses presented in the main text include data from January 9 to February 14, 2023 (inclusive). We excluded February 15th to February 28th, 2023 (inclusive) because there was a gap in data from February 15th to February 23rd, 2023 (inclusive) as one of the 8 feeders had a damaged circuit board during this period. Furthermore, chickadees can begin to establish breeding territories in early February, which can initiate winter flock break up (Smith, 1992). Thus, for the analysis presented in the main test, we did not include February 24th to 28th, 2023 (inclusive).

To confirm that this did not unduly influence results, we ran analyses that did include the dates from February 15th to 28th, 2023 (inclusive). We found evidence that indeed an alternative biological process is occurring during February 24th to 28th, 2023 (inclusive). The temperature effects were diminished (see Supplementary Table S1 for model output), however, we found that on the coldest day in our dataset (-26.8°C on February 24th), there was low feeder visitation (see Supplementary Figure S2). This suggests that during this time, chickadees are less dependent on the feeders regardless of temperature (i.e., flock break up has commenced).

Supplementary Text S3. Post hoc analysis of sex-related differences in annual survival.

Given that we observed sex-related differences in space-use and feeding rate and found that a higher feeding rate predicts a higher survival likelihood, we wanted to evaluate whether underlying differences in male and female survival, potentially masked effects of space use on survival.

We constructed a generalized linear model (GLM) for survival (yes/no) as a function of sex fitted with a binomial error distribution in the R statistical environment v. 4.0.3 (R Development Core Team, 2020) using the RStudio interface (R Studio Team, 2020).

We found evidence that males were less likely to survive to the next fall (log odds ratio = 0.15, CI = -0.33, 0.62) than females (log odds ratio =0.50, CI=0.02, 1.00).

Table S1. LMM results for unique feeder count and feeding rate from January 9th to February 14th, 2023 (inclusive), and February 24rd to 28th, 2023 (inclusive). Note, dates from February 15th to 23rd, 2023, are not included because one feeder had a broken circuit board during this time.

	Unique Feeder Count (number of unique feeders visited per day)	Feeding Rate (total number of feeder visits per day)
Fixed effects	*β (95% CI)*	*β (95% CI)*
Female – Juvenile	1.22 (1.11, 1.30)	58.36 (51.47, 67.03)
Female – Adult	1.18 (1.07, 1.28)	62.05 (53.49, 69.89)
Male – Juvenile	1.32 (1.18, 1.39)	67.58 (58.58, 75.54)
Male – Adult	1.12 (1.02, 1.22)	70.46 (62.16, 77.99)
Female – Juvenile : Temperature	-0.02 (-0.06, 0.02)	-6.62 (-9.17, -3.58)
Female – Adult : Temperature	-0.02 (-0.05, 0.03)	0.12 (-3.56, 2.57)
Male – Juvenile : Temperature	0.03 (-0.009, 0.07)	-12.41 (-15.36, -9.67)
Male – Adult : Temperature	0.02 (-0.01, 0.07)	-6.73 (-9.97, -4.43)
Random Effects	*σ (95% CI)*	*σ (95% CI)*
Transponder Hex Code N=138	0.08 (0.08, 0.09)	567.85 (531.63, 603.01)
Residual N= 5625	0.12 (0.12, 0.13)	628.31 (605.22, 652.32)
Repeatability	*r (95% CI)*	*r (95% CI)*
Transponder Hex Code N=138	0.41 (0.36, 0.47)	0.47 (0.41, 0.53)

Note, intercept values for Age-Sex categories are estimated at 0°C, and temperature was standardized prior to analysis, therefore estimate effect sizes are for 1 s.d. change in temperature (i.e., 5.74°C).

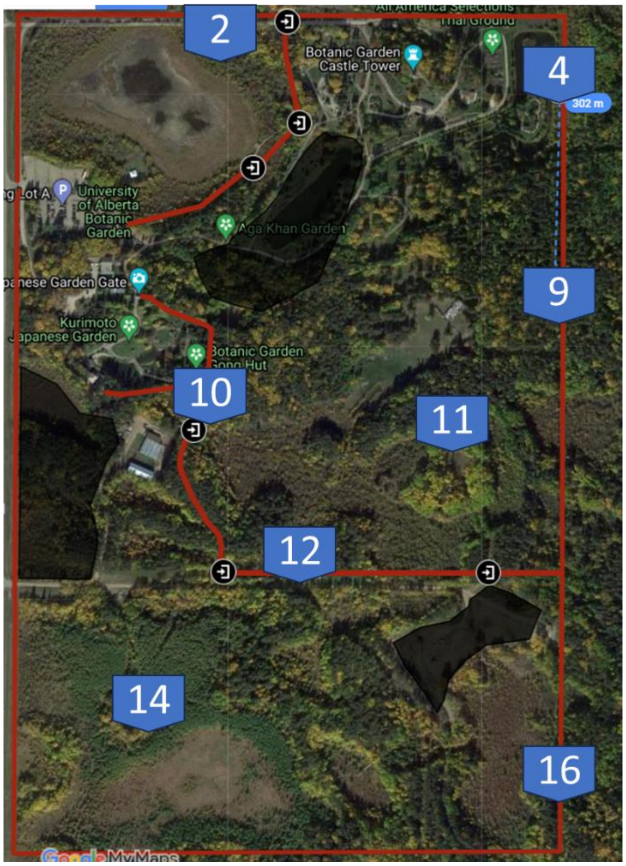

Figure S1. Feeder map at the University of Alberta Botanic Gardens. Feeder locations are labeled with their respective numbers (2, 4, 9, 10, 11, 12, 14, and 16). Note that feeder 14 (i.e., "thermal feeder") was removed from this study's dataset (see methods in main text for further details). Each feeder was at least 270m apart to reflect approximate chickadee flock sizes. For reference, the distance between feeder 4 and 9 is 302m. Map constructed by [insert name] with feeder labels added by [insert name].

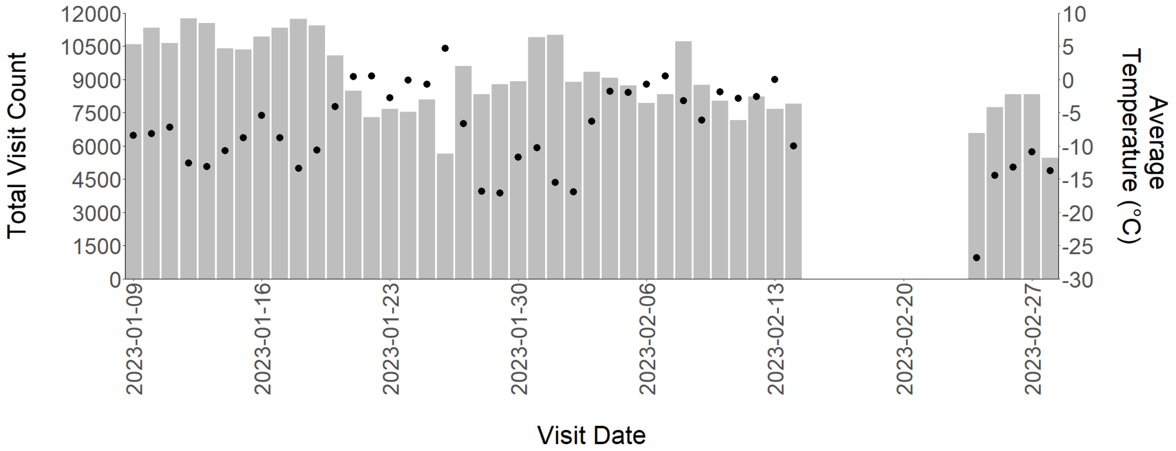

Figure S2. Total number of daily feeder visits and average daily temperature from January 9th to February 28th, 2023 (inclusive). The total number of daily feeder visits (represented by the grey bars) is summed across age-sex groups per day. The average daily temperature (represented by the black points) is provided by Alberta Agriculture and Forestry, ACIS: https://agriculture.alberta.ca/acis. No data were collected February 15th to 23rd due to a technical glitch.

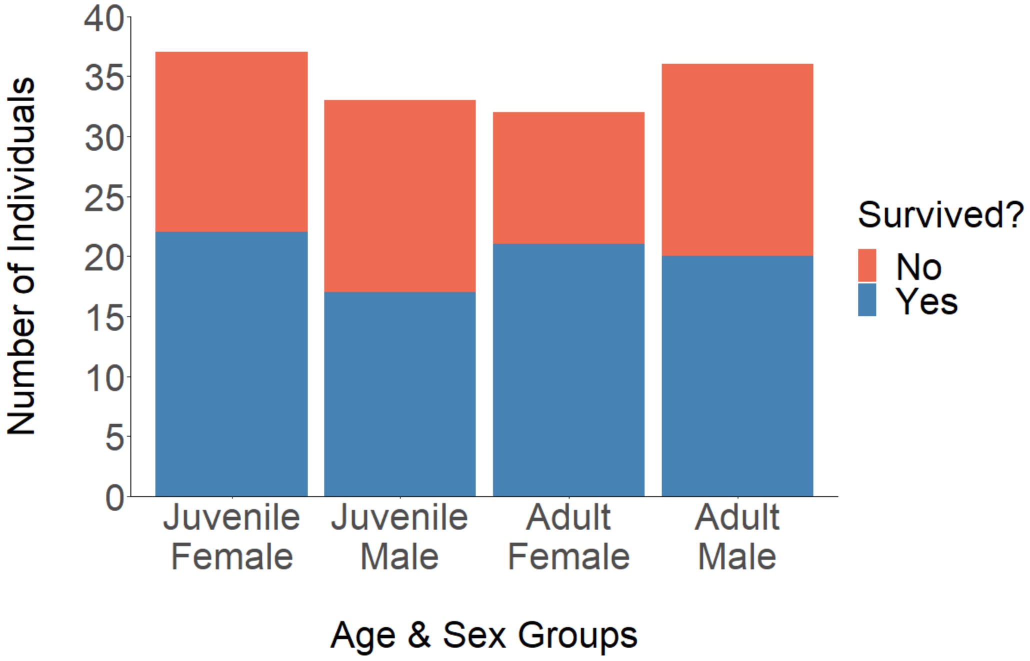

Figure S3. Bird annual survival based on age-sex groups. Juvenile females had a survival rate of 59.46% ($N_{survived}$=22, N_{died}=15), juvenile males had a survival rate of 51.52% ($N_{survived}$=17, N_{died}=16), adult females had a survival rate of 65.63% ($N_{survived}$=21, N_{died}=11), and adult males had a survival rate of 55.56% ($N_{survived}$=20, N_{died}=16)

Supplementary References

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