

**CONSISTENCY IN SUPPLEMENTAL FOOD AVAILABILITY AFFECTS THE SPACE  
USE OF WINTERING BIRDS**

A Thesis

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By

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## **ABSTRACT**

Across the globe, millions of people feed wild birds and this practice has profound implications for many bird species. To better understand the effects of this supplemental feeding, many researchers have compared birds with access to inexhaustible supplemental food to those without access. However, the consistency of supplemental food availability varies with people's provisioning habits because some people fill their feeders daily while others do so sporadically. As the consistency of food changes, a bird's foraging strategy, including its use of space, should change. To determine how space use varies with the consistency of supplemental food, we surveyed three species with access to experimental feeders that provided constant, pulsed, or no access to food. We conducted these surveys at two locations—near and far from the feeder—within nine sites to determine differences in space use among and within sites. Access to supplemental food, regardless of feeding regime, anchored the movements of each species near the feeders. However, the different feeding regimes had different effects on space use. Birds with constant access were continually anchored near the feeders while the birds with pulsed access were temporarily anchored near the feeders. We found that for only one of the three species, black-capped chickadee, that there were two more birds near feeders with pulsed access when food was available compared to near feeders with constant access. Supplemental feeders act as spatial anchors but do so in different ways across species and feeding regimes with potentially different implications for survival and population dynamics.

## **BIOGRAPHICAL SKETCH**

Rachael P. Mady completed a Bachelor of Science degree at Towson University in 2016, worked as a naturalist in 2017, and then arrived at Cornell University in 2018. She came to Cornell to expand and deepen her field research skills, learn more about citizen science, and gain teaching experience. She pursued a Master of Science degree in Natural Resources and worked as a Graduate Research Assistant for Bird Cams Lab, a project funded by the National Science Foundation that aims to provide an online space for scientists and Bird Cam viewers to “co-create” scientific investigations.

While at Cornell, Rachael learned new and improved upon existing research skills she had begun to develop as an undergraduate student in two Research Experiences of Undergraduates (REU) programs. For her thesis, she designed and conducted a field research experiment to better understand how consistency in the availability of supplemental food at birdfeeders influences the space use and foraging strategies of wild birds. As is the case for many field research projects, she navigated several obstacles, including a technological one that in the end prevented her from quantifying the foraging strategies of birds. In addition to her main project, she collaborated with Vicki Martin, a social scientist, to distribute a national survey to describe variation in the availability of supplemental food at birdfeeders food across the United States.

As a Graduate Research Assistant, Rachael interacted with thousands of volunteer participants in all parts of the scientific process, from observation to data collection to sharing the results. She learned how to successfully communicate about science in an informal setting through emails, forums, blog posts, and live question and answer sessions. Working with researchers, communicators, and social scientists on the Bird Cams Lab team, she also learned

about the complexities of citizen sciences, such as data quality concerns and different ways to engage with participants. Rachael enjoyed working as the research assistant to Bird Cams Lab because the work allowed her to intersect science, engagement, and teaching in one space.

She also worked as a teaching assistant for the Field Methods in Avian Ecology course as well as an organizer and leader for bird banding workshops and lessons at a local elementary school. She taught undergraduate students basic field ornithological skills and how to conduct a research project. On several occasions, Rachael organized and led workshops in which she did bird banding demonstrations for people of all backgrounds and ages. She learned how to distill complicated information in succinct ways and how to engage the public in a topic they might not know much about.

After graduating from Cornell, Rachael will continue to work with the Bird Cams Lab team during a one-year extension of the original National Science Foundation grant. Long term, she will continue to share her love of birds with others and seek out opportunities to intersect science with outreach or education.

## **DEDICATION**

I dedicate this thesis to my mother, Joyce Hutton Mady.

She is the most kind, loving, and selfless person I know.

She's always supported me and now gets just as excited, if not more,  
as I do when seeing new birds.

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Because this work is based on a field research experiment, there are many people to thank for helping me with the logistics and fieldwork. First and foremost, I would like to thank all the homeowners that agreed to not fill their bird feeders so that I could use sites located near their residences. Without their cooperation, my field research project would have been non-starter. Thank you as well to Justin Cleveland for talking to sponsors so that I could raffle off binoculars and other items to help convince homeowners to not fill their feeders. Thank you to everyone that helped me secure access to the sites themselves that I used during this study: Todd Bittner, Lawrence Carlisle, Timothy Lynn Van Deusen, John Clancy, James Gustafson, and Nicholas Vail. I am so grateful for the following people that came out to help me set-up my experiment and maintain the experiment, sometimes on days that were bitter cold: Eric Hughes, Facundo Fernandez-Duque, Zena Casteel, Yuting Deng, Sarah Toner, Kevin Ebert, Alexandra Palting, Taylor Brown, Joyce Mady, Charles Eldermire, Lucy Eldermire, Wyatt Eldermire. You all helped me hold onto my sanity. Thank you especially to Charles, Lucy, and Wyatt Eldermire for keeping my experiment running so that I could visit my family for the holidays. The experiment would have also not been possible without the seed provided by Wild Birds Unlimited and delivered by Jeffrey Payne and Benjamin Wheeler.

I am extremely grateful that during my time at Cornell I found a warm and caring community of people where I live and work. Thank you to my housemates (Anna Lello-Smith, Maddie Ore, Tayler Brooks, Bethany Jorgensen) for the countless nights of family dinners and being there for me in the best and worst of times. Thank you to my friends that listened, encouraged, and became role models for me. Thank you especially to Gemma Clucas and Jen Walsh-Emond for including me on after-work runs, asking about my day, giving me advice, and embodying the balance between work and life. Thank you to the Bird Cams Lab team (Miyoko

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## INTRODUCTION

Supplemental feeders are part of the environment that many birds experience (Wilson 2001) and are so widespread that feeding birds has been referred to as a “large-scale experiment” (Jones and Reynolds 2008). In the United States, more than 57 million people feed wild birds and spend greater than four billion U.S. dollars on bird food annually (U.S. Department of the Interior et al. 2016). An estimated 55% of households in the U.K. and 36-48% in Australia provide food for birds (Ishigame and Baxter 2007; Orros and Fellowes 2015). The wide-spread provisioning of supplemental food has changed the overall food availability for many species such that bird communities around feeders are altered, potentially leading to large-scale population changes (Plummer et al. 2019). Species with access to supplementary food have been observed to expand their ranges (Job and Bednekoff 2011; Greig et al. 2017), increase in local abundance (Boutin 1990; Wilson 1994; Wilson 2001; Galbraith et al. 2015; Sonne et al. 2016;), alter reproductive output (Robb et al. 2008), change their fat reserve levels (Rogers and Heath-Coss 2003), and decrease parasite loads (Knutie 2020). In the presence of feeders, some species participate less in mixed-species flocking (Grubb 1987; Kubota and Nakamura 2000), are less fearful of humans (Feng and Liang 2020), and alter their winter territorial behavior (Smith 1991).

A characteristic of supplemental feeding that has received very little attention is the consistency with which this food is provided (Crates et al. 2016). Across the bird-feeding landscape, the availability and predictability of supplemental food varies because some people fill their feeders daily while others do so only intermittently (Gaston et al. 2007; Horn and Johansen 2013). In contrast, most supplemental feeding studies have followed a similar methodology in which birds with constant access to supplemental food are compared to birds without any access (but see Galbraith et al. 2015; Crates et al. 2016; Malpass et al. 2017).

Moreover, previous supplemental feeding experiments have only assessed the effects of one feeding regime at a time, rather than comparing different approaches to providing supplemental food.

A feeder may become a stronger “spatial anchor” as the amount and consistency of supplemental food increases because of the increased reliability of foraging success. The feeder “anchors” the movements of birds accessing the food to be in the immediate area around the feeder (Roth and Vetter 2008). With consistent access to abundant supplemental food, birds may perform area-restricted searching such that they alter their movements and frequently return to the location, in this case a feeder, where they previously successfully foraged (Smith 1974; Tinbergen et al. 1967). Birds may also decrease their home range size because they need to cover less area to obtain needed energy (Roth and Vetter 2008). For instance, dark-eyed junco (*Junco hyemalis*) flocks with constant access to supplemental food at a feeder travelled less than half the distance and had approximately half the home range size of flocks with no access (Roth and Vetter 2008). This has also been confirmed in ungulates, such that the greater the amount of provided supplemental food in an area, the smaller the home range size (Jerina 2012).

Compared to animals with constant food access, animals with access to inconsistent or unpredictable food may be more motivated to forage across wider spaces and do so more actively (Anselme et al. 2017; Anselme and Güntürkün 2019) . In an aviary experiment with spotted munia (*Lonchura punctulata*), individuals with intermittent access to food increased their activity levels and food intake rate when food was available compared to the activity levels and food intake rate of birds with constant access to food (Srivastava et al. 2015). Similarly, as food availability became highly variable, marsh tits (*Poecile palustris*) increased their foraging effort compared to when food availability was more constant (Hurly 1992). At supplemental feeders,

inconsistent supplemental food availability may temporarily spatially anchor birds' movements, altering their space use as they exploit the ephemeral resource and focus more of their foraging activity at the feeder while the food is available.

The objective of this study was to determine if space use by free-living birds varies in response to different feeding regimes that alter temporal availability of supplemental food. We surveyed bird species that commonly visit feeders with access to experimental feeders that provided constant, pulsed, or no access to supplemental food. To capture variation in space use among and within sites, we surveyed birds near and far from feeders. Regardless of the feeding regime, we predicted that if access to supplemental food spatially anchors birds, then (1) there would be more birds at sites with food compared to sites without, and (2) that within sites there would be more birds near compared to far from feeders. With respect to the different feeding regimes, we tested two sets of predictions. If the birds are more spatially anchored to constant sources of supplemental food, then there would be (1) more birds at these sites, (2) more birds near these feeders, (3) and a greater difference in the number of birds near and far from these feeders at these sites. If birds are more spatially anchored to pulsed sources of supplemental food, then when food becomes available there would be (1) more birds near these feeders, (2) and a greater difference in the number of birds near and far from these feeders.

## MATERIALS AND METHODS

Research was conducted at nine study sites in Tompkins County, New York, USA (42° 26' 35" N, 76° 30' 04" W). We focused on three common species that regularly visit bird feeders: black-capped chickadee (*Poecile atricapillus*, hereafter chickadee), tufted titmouse (*Baeolophus bicolor*, hereafter titmouse), and white-breasted nuthatch (*Sitta carolinensis*, hereafter nuthatch). We installed experimental feeders and surveyed these species at forested sites that met the following criteria: forest stands bordered a road or field, were predominantly deciduous or a mix of deciduous and coniferous tree community, had similar land-use history and forest age, and had few nearby private residences. Each site was separated from adjacent sites by a minimum 300-m gap because gap crossing in these species rarely exceeds that distance (Grubb and Doherty 1999; Bailey et al. 2018). We confirmed that birds had little to no access to other anthropogenic food sources by coordinating with private homeowners within a 500 m radius of each feeder location, a radius that encompasses an area of 79 hectares and is much larger than observed winter home range sizes of the focal species (chickadee: 8.8-22.6 ha, Odum 1942; titmouse: 4.3-10.5 ha, Wilford 1977; nuthatch: 10-20 ha, Butts 1931). For part of the experiment, deer management activities did take place at one site where automated feeders were set-up to drop cracked corn (a non-preferred food source for our focal bird species) on the ground to attract deer.

Each of the nine feeding sites was approximately 55 m from the forest edge (mean  $\pm$  SE = 54.89  $\pm$  3.3 m). We hung one tube feeder 2 m ( $\pm$  0.03 m) from the ground at each site, positioned such that small mammals could not access the feeders by jumping from nearby trees. We designed the feeders following Bridge and Bonter (2011). We filled feeders with black-oil sunflower seeds, a type of food preferred by the focal species (Tryjanowski et al. 2018), so that supplemental food was available daily from August to the start of the experiment. To aid banding

efforts for a separate study, we filled a platform feeder or an additional tube feeder next to the experimental feeder prior to initiating the experiment.

To minimize bias, we used a stratified random design to assign which locations received each of the three food-availability treatments. We grouped sites by similarity in location, forest patch size, type of edge habitat (with a road or field), and cardinal direction of forest edge into groups of three. Within each group we randomly assigned one of three treatments: constant access to food (available every day), pulsed access to food (available three consecutive days a week), and control (feeder present but no food available). To create the pulsed treatment, the tube opening was closed with a piece of sheet metal and duct tape each Thursday and opened by removing the sheet metal each following Tuesday. We aimed to open and close the three pulsed feeders in the same order and at the same time after sunrise so that food was available for the same amount of time across pulsed sites and throughout the study period. Occasionally poor weather conditions limited site accessibility such that pulsed feeders were opened in a different order or later in the day (N = 4 open/close cycles). Depending on the completion of banding at a site, we began experimental treatments in the last week of October and first two weeks of November 2018 by closing pulsed feeders and emptying control feeders.

The same observer conducted point count surveys of the focal species at locations “near” (within 10 m) and “far” ( $206 \pm 5$  m, range: 167-226 m) from the feeder at each site from November 2018 - March 2019 (Fig. 1). The near and far points were selected to be approximately 50 m from the nearest forest edge. The “near” location allowed us to observe the birds in the area around the feeder with minimal disturbance, and the “far” location was the farthest possible distance at each site we could go while remaining in the same habitat. All birds seen and heard within a 50-m radius were recorded during 5-minute point counts. The observer

conducted the surveys twice a week such that they conducted weekly surveys at the pulsed-food locations on days where pulsed feeders did and did not have food available (e.g. Monday and Wednesday). The observer also rotated through the three groups, each consisting of three sites (constant, pulsed, control), such that they surveyed one group a week. To minimize effects of human presence on bird activity, the observer waited two minutes after arrival to begin each survey. Precipitation (light rain, heavy rain, light snow, heavy snow, none), wind speed (Beaufort scale 0-5), and ground snow cover (yes or no) were recorded for each count. Hourly minimum temperature data was obtained from a weather station located < 10 km from all sites (Northeast Regional Climate Center 2019). All surveys were conducted before noon, and no surveys were conducted in high winds, heavy rain, or periods of heavy snowfall.

## STATISTICAL ANALYSES

To investigate how space use varied with supplemental food availability, we ran generalized linear mixed effects (GLMM) models using the *glmmTMB* package (Brooks et al. 2017) in R 3.5.3 (R Core Team 2019) with the number of birds detected as the response variable. We ran all models with a zero-inflation component because we detected zero birds on several surveys, and scaled and centered continuous predictor variables to reduce collinearity and improve model fit (Cheng et al. 2010; Schielzeth 2010). To determine which error distribution to use for each species, we calculated the mean and variance of the response variable for each treatment level. If the variance was less than twice the mean, we fit models with the Poisson distribution (titmouse and nuthatch), and if the variance was greater than the mean we fit models with the negative binomial distribution (chickadee) (Bolker et al. 2009; Brooks et al. 2017).

Several predictor variables were included in the model to account for potential causes of variation in detectability of birds. We included site as a random variable because each site, which includes both the “near” and “far” locations, was sampled multiple times (range 11 - 12). We also included Julian date (defined as days since November 1) and time of day (calculated as minutes since sunrise) as continuous, linear predictors, because we expected bird detections to vary with the season and time of day.

We conducted a preliminary analysis to identify weather variables correlated with bird counts for use in further analyses presented in this paper. We modelled the combined number of individual birds of all three focal species detected near feeders as a function of a suite of weather variables recorded during each count that we expected to influence birds’ use of supplemental food: minimum temperature, wind speed, precipitation, and snow cover (Grubb 1975). Before fitting the model, we confirmed that there was variation within these variables by calculating the

coefficient of variation for the continuous variables (Lüdtke 2019) and the coefficient of unalikeability for the categorical variables (Redd 2019). We also confirmed that the variables were not correlated using Pearson's correlation coefficient, logistic regression, and biased-corrected Cramer's V (Mangiafico, 2019; R Core Team 2019). Because the model was unable to successfully estimate effects of precipitation (i.e. the effect of one precipitation class had an estimated standard error almost 400 times larger than the parameter estimate), we removed the variable and re-ran the model. The combined number of nuthatches, titmice, and chickadees appeared to be correlated with snow cover ( $\chi^2 = 3.92$ , Df = 2, P = 0.048), but not with minimum temperature or wind speed (P  $\geq$  0.255). Therefore, we only included snow cover in subsequent analyses.

For each species we tested our predictions with three main models. (1) To determine if birds were more spatially anchored to sites with access to supplemental food (constant or pulsed) compared to sites without access (control), we combined the counts of birds at the two survey locations within a site on each sampling day and modeled this number of birds detected as a function of treatment (constant access, pulsed access, control), minutes after sunrise, Julian date, and snow cover, with site as a random variable. (2) To test for differences in the degree of spatial anchoring across food treatments, we limited the data set to counts conducted within 10 m of the feeder and split the treatment levels into constant, pulsed with food available, and pulsed with no food available. We then modeled the number of birds seen near a feeder as a function of treatment, with the same covariates and random variable as the first model. (3) To further determine if there were more birds near feeders compared to far away from feeders and if this difference between near and far differed between supplemental food treatments, we modeled the number of birds seen at a survey point as a function of the interaction between treatment

(constant, pulsed with food available, pulsed with no food available) and location (near, far) with the same covariates as the above models.

For this third model, because the response variable was the number of birds seen at a survey location, the first step in running this analysis was to determine the most appropriate random effects. Our surveys were conducted in a manner that required us to account for non-independence of surveys: each site had two survey locations that were visited within the same day, and each site was visited twice within the same week. Thus, we examined the utility of including four random effects: site-within-day-within-week, day-within-week, week, and site-within-day. The inclusion of week also allowed us to capture any potential variation that was not accounted for by the linear relationship described by an effect of Julian date. For chickadees and nuthatches, the site-within-day random effects explained 7-12 orders of magnitude greater variance than any of the three other random effects. Thus, in the final model for chickadees and nuthatches we only included site-within-day as the random effect. For titmice, we found variance of similar magnitude explained by week and site-within-day, with the other two random effects (site-within-day-within week and day-within week) explaining 8 to 9 orders of magnitude less variance. In the final model for titmice we only included week and site-within-day as random effects.

In addition to these analyses, we tested for statistical support for a pattern perceived during surveys: an increase in the number of birds detected near pulsed feeders without food available as the season progressed. We modeled the number of birds detected near a feeder as a function of the interaction between treatment (constant, pulsed with food available, pulsed with no food available) and Julian date with minutes after sunrise and snow cover as covariates and site as the random variable.

We confirmed that model assumptions were met using a simulation-based approach with the *DHARMA* package (Hartig 2019). Following Bolker et al. (2009), we performed Type II Wald Chi-square tests to assess the statistical importance of each fixed effect for each model. We used the *emmeans* package (Lenth 2019) to calculate the Estimated Marginal Means (EMMs) with their pairwise differences for the levels of location and treatment. All EMMs and pairwise comparisons were calculated by marginal averaging on the log scale (Lenth 2019). For the treatment×date model, we used `emtrends()` from the *emmeans* package (Lenth 2019) to calculate and statistically compare estimates of the slopes among the three treatments.

To understand the biological relevance of the results, we visualized the EMMs on the response scale using the *ggplot2* package (Wickham 2016). EMMs and the limits of their 95% confidence intervals were back-transformed to the response scale after they were calculated on the log-scale. Thus, the confidence intervals in the graphs are for visualization purposes and do not reflect the t-tests performed in the pairwise comparisons between the EMMs. To visualize the interaction between treatment and Julian date, we used the `ggemmeans()` and `plot()` functions from the *ggeffects* package (Lüdtke 2018).

## RESULTS

Each of the nine study sites was surveyed 11-12 times, resulting in 204 point counts. The number of detected birds at a site differed among treatment (constant access, pulsed access, or control) for each species (chickadee:  $\chi^2 = 55.20$ , Df = 2,  $P < 0.001$ ; titmouse:  $\chi^2 = 9.46$ , Df = 2,  $P = 0.009$ ; nuthatch:  $\chi^2 = 10.62$ , Df = 2,  $P = 0.005$ ). At sites with access to food, constant or pulsed, we detected on average five more chickadees and one to two more nuthatches compared to control sites that lacked supplemental food (Table 1, Fig. 2). For titmice, there was little difference between sites with pulsed access to food and control sites, but we detected an average of one to two more titmice at sites with constant access to food compared to control sites (Table 1, Fig. 2). For each species, the number of birds detected at sites with pulsed access was similar to the number of birds detected at sites with constant access (Table 1, Fig. 2). The potential covariates of sampling date, time of day (minutes after sunrise), and presence/absence of snow cover were not related to the number of birds detected for any species (all  $P \geq 0.149$ ).

Limiting the dataset to counts conducted within 10 m of feeders, there was a relationship between the number of birds detected and treatment (constant access, pulsed access with food available, pulsed access with no food available) for each species (chickadee:  $\chi^2 = 21.80$ , Df = 2,  $P < 0.001$ ; titmouse:  $\chi^2 = 12.76$ , Df = 2,  $P = 0.002$ ; nuthatch  $\chi^2 = 14.08$ , Df = 2,  $P = 0.001$ ). Similar numbers of titmice and nuthatches were detected near feeders with constant access and feeders with pulsed access with food available, but there were on average two more chickadees near feeders with pulsed access with food available compared to near feeders with constant access (Table 2, Fig. 3). When we compared the number of birds detected near feeders with constant access and feeders with pulsed access with no food available, we found that there were on average three more chickadees, two more titmice, and two more nuthatches near feeders with

constant access (Table 2, Fig. 3). There were also on average four more chickadees, one more titmouse, and two more nuthatches near feeders with pulsed access with food available compared to no food available (Table 2, Fig. 3). Neither time of day nor the presence/absence of snow cover were strongly correlated with the number of birds detected near feeders for any species (all  $P \geq 0.063$ ). Sampling date was not correlated with the number of titmice or nuthatches (all  $P \geq 0.718$ ), but was correlated with the number of chickadees, with more chickadees detected as the season progressed ( $\chi^2 = 4.15$ , Df = 1,  $P = 0.042$ ).

Within sites, the number of detected birds was related to the interaction between location (near, far) and treatment (constant access, pulsed access with food available, pulsed access with no food available) for chickadees and nuthatches (chickadee:  $\chi^2 = 7.84$ , Df = 2,  $P = 0.020$ ; nuthatch:  $\chi^2 = 14.07$ , Df = 2,  $P < 0.001$ ). For titmice, treatment and location did not interact and instead were additively related (Treatment  $\times$  Location:  $\chi^2 = 4.84$ , Df = 2,  $P = 0.089$ ; Treatment:  $\chi^2 = 12.70$ , Df = 2,  $P = 0.002$ ; Location:  $\chi^2 = 32.94$ , Df = 2,  $P < 0.001$ ). On average there were four to six more chickadees, one to two more titmice, and one to two more nuthatches detected near (within 10 m) compared to far from feeders when food was available (pulsed or constant access) (Table 3). We did not find differences in the number of birds detected near and far from pulsed feeders with no food available for any species (Table 3). When we compared the difference in the number of birds detected near and far from feeders, we found that this difference was the same for sites with constant access to food and sites with pulsed access to food when food was available for each species (Table 4, Fig. 4). Sampling date, time of day, and the presence/absence of snow cover were not correlated with the number of birds detected for any species (all  $P \geq 0.114$ ).

The number of individual chickadees detected near feeders was related to the interaction between sampling date and treatment (constant access, pulsed access with food available, pulsed access with no food available) ( $\chi^2 = 9.81$ , Df = 2, P = 0.007). As the season progressed, the number of chickadees near feeders with pulsed access to food with no food available converged with the number of chickadees near feeders with pulsed access to food with food available and the number of chickadees near feeders with constant access to food (Fig. 5). The increase in the number of chickadees near feeders with pulsed access to food without food available was greater across the season than the increase at the other treatment sites (Table 5, Fig. 5). For titmice and nuthatches, neither the interaction nor additive relationship between treatment and sampling date were correlated with the number of birds (Treatment  $\times$  Date: both P  $\geq$  0.058; Treatment: both P  $\geq$  0.363; Date: both P  $\geq$  0.396). Time of day and the presence/absence of snow cover was not strongly related to the number of birds detected near feeders for any species (all P  $\geq$  0.058).

## DISCUSSION

We found not only that the presence of supplemental food, but also the consistency with which this food was available, alters space use by resident birds in winter. Chickadees, nuthatches, and titmice with constant access to supplemental food were continually anchored near the feeders while those with pulsed access were temporarily anchored (Fig. 3; Fig. 4). This spatial anchoring is a logical result of supplemental feeding because the greater the food availability, the sooner an individual can meet its energy requirements, rest, and avoid being exposed to predators (Brodin and Clark 2007). On days where there was no food available at the feeder with pulsed access, the birds would have had to move more and cover a larger area compared to days when food was available or compared to the birds with constant access to food (Fig. 3). Our results build upon previous research wherein dark-eyed juncos with access to supplemental food were found to move less and have smaller winter home ranges compared to flocks without access (Roth and Vetter 2008). Similarly, Eurasian nuthatches (*Sitta europaea*) with access to supplemental food had smaller territories compared to those without access (Enoksson and Nilsson 1983).

For chickadees, we found that the feeders with pulsed access attracted more birds on the days on which food was available compared to the feeders with constant food access (Fig. 3). This greater anchoring of chickadees near feeders with pulsed access to food may be due to the chickadees with pulsed access being more motivated to exploit the temporary superabundance of food compared to the chickadees with constant access. The overall food availability for chickadees with pulsed access was more variable such that motivation to forage when food was located was potentially higher (Anselme et al. 2017; Anselme and Güntürkün, 2019). Chickadees with constant access could have been less motivated to forage, since they had a more consistent

supply of food, and could instead prioritize reducing predation risk by resting and spreading their foraging throughout the day, balancing the starvation-predation trade-off (McNamara 1990; Bonter et al. 2013).

Alternatively, the higher counts of chickadees when food was available at the pulsed feeders may not have been a result of more chickadees using the feeders, but instead the chickadees having a higher probability of detection due to their increased rate of feeder visitation and caching seeds nearby. Previous work has found that the birds with unpredictable access to food forage more actively and cache more seeds compared to birds with constant access (Pravosudov and Grubb 1997; Srivastava et al. 2015 but see Karpouzou et al. 2005). Barnea and Nottebohm (1995) observed flocks of black-capped chickadees foraging at feeders and found that individuals stored the majority of seeds within 15 m of the feeder. Caching near feeders has also been observed in the willow tit (*Poecile montanus*), with individuals rarely storing seeds farther than 50 m from the feeders (Brodin 1992). In contrast, the chickadees at the sites with constant access had an overall more consistent food supply such that they could afford to spread their foraging effort throughout the day (Bonter et al. 2013) and cache fewer seeds, leading to fewer detections per count.

This caching behavior, changes in the costs and benefits of foraging behaviors, and “time-space” learning, could explain why, as the season advanced from November to March, we also saw an increase in the number of chickadees near the feeders with pulsed access on days when food was *not* available. In November, on days with no food available, there were few to no chickadees near pulsed feeders, but in March, the number of chickadees became comparable to the numbers detected on days when food was available (Fig. 5). Later in the season, the chickadees were potentially accessing their caches that they had stored and doing so more

frequently as the number of caches around the feeder increased with time. Alternatively, as the season progressed and the natural food supplies depleted, the benefit of finding it full increased, leading to the birds checking it more often. Even still, the chickadees could have learned to check the feeders with pulsed access more often and/or closer to the day that we opened the feeders. Time-place learning reflects an animal's ability to navigate to resources based on temporal and spatial cues (Crystal 2009) and has been demonstrated in other bird species. Biebach et al. (1989; 1994) experimentally showed that captive garden warblers (*Sylvia borin*) trained to expect food at certain feeders at designated times continued to choose those feeders, even when food became freely available at all feeders at all times. Tello-Ramos et al. (2015) confirmed these findings in the field, observing that rufous hummingbirds (*Selasphorus rufus*) learned to primarily visit one of four artificial flower patches at the time of day that the food was available. When we designed the study, we did not expect any of the focal species to be able to perceive the predictability of opening the pulsed feeders at the same day and time each week. Previous work has found evidence that chickadees remember the locations of their caches for at least 28 days (Hitchcock and Sherry 1990), but there is no evidence of how well they are able to perceive week-to-week patterns of food availability. To better compare the effects of feeding regimes that differ in predictability and test the time-space learning capabilities in species like chickadees, future work should test different feeding regimes such that supplemental food availability is unpredictable in one treatment.

Overall, our results provide insight into how the space use of birds shifts in response to variation in the availability of supplemental food and raises two topics for further investigation. First, future work should assess the effects of differences in the availability of supplemental food feeding regimes in more developed areas, where there is potentially less natural food and a

greater influence of the type of supplemental feeding regime. We conducted the experiment in a non-urban setting to minimize the influence of other supplemental food resources, selecting sites as far as possible from homes and working with homeowners near our sites to not feed birds during the experiment. By doing so, we increased the likelihood that birds only had access to our supplemental feeders at our sites. However, this approach also meant that the birds at our sites likely had access to greater natural food supplies than birds in more developed contexts. Second, we were not able to identify or follow individually marked birds, such that we could not quantify the potentially large variation in individual use of supplemental food that has been found in other species (Crates et al. 2016; Galbraith et al. 2017). This also meant that we could not differentiate between individuals with home ranges immediately around the feeder and those farther away. Brittingham and Temple (1992) and Wilson (2001) observed over a hundred individuals using feeders that provided constant access to food, a number far exceeding the number of individual black-capped chickadees typically seen in winter flocks (3-12 individuals, Foote et al. 2010). In our study the feeders with constant access may have attracted individuals from farther away compared to the feeders with pulsed access, influencing the overall abundance and our measure of subsequent space use. To capture individual variation and to differentiate between winter flock home ranges, future work should use RFID-enabled feeders or radiotelemetry to follow individual birds and quantify their movements (see Roth and Vetter 2008; Cox et al. 2016). In summary, our work elucidates how birds use space differently when exposed to different supplemental feeding regimes. The pulsed and constant feeding regimes anchored birds near feeders differently and potentially have different effects on species survival and population dynamics. While evidence suggests that the overall practice of bird feeding can affect several aspects of a bird's life history, including reproductive success (Robb et al. 2008) and survival

(Brittingham and Temple 1988), and alter large-scale movement patterns like migration (Plummer et al. 2015; Greig et al. 2017), we still know little about how variation in the amount and consistency of supplemental feeding might affect birds. People around the world differ in how they provide food, such that some provide a predictable, constant resource and others provide a less predictable, less consistent resource (Gaston et al. 2007; Davies et al. 2012; Horn and Johansen 2013). If we want to understand how the “large-scale supplemental feeding experiment (Jones and Reynolds 2008) is actually affecting birds, we need to better assess the effects of different feeding regimes.

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## TABLES AND FIGURES

Table 1. The results from pairwise tests of treatment differences in the Estimated Marginal Mean (EMM) numbers of birds detected at the site-level (i.e. number of birds detected at the two survey locations at each site combined) for each species. Estimates of the difference in the EMM and their Standard Errors (SE) are given on the log scale. Comparisons with P-values less than or equal to 0.05 in bold.

<i>Species</i>	<i>Comparison</i>	<i>Estimate</i>	<i>SE</i>	<i>Df</i>	<i>T</i>	<i>Lower CL</i>	<i>Upper CL</i>	<i>P</i>
<b>Chickadee</b>	<b>Constant – Control</b>	<b>2.46</b>	<b>0.33</b>	<b>93</b>	<b>7.37</b>	<b>1.67</b>	<b>3.24</b>	<b>&lt;0.001</b>
	<b>Pulsed – Control</b>	<b>2.43</b>	<b>0.35</b>	<b>93</b>	<b>6.99</b>	<b>1.61</b>	<b>3.25</b>	<b>&lt;0.001</b>
	Constant – Pulsed	0.03	0.16	93	0.15	-0.35	0.35	0.987
<b>Titmouse</b>	<b>Constant – Control</b>	<b>2.28</b>	<b>0.74</b>	<b>94</b>	<b>3.07</b>	<b>0.51</b>	<b>4.04</b>	<b>0.008</b>
	Pulsed – Control	1.36	0.75	94	1.82	-0.42	3.14	0.169
	Constant – Pulsed	0.92	0.64	94	1.44	-0.60	2.43	0.323
<b>Nuthatch</b>	<b>Constant – Control</b>	<b>1.56</b>	<b>0.49</b>	<b>94</b>	<b>3.20</b>	<b>0.40</b>	<b>2.72</b>	<b>0.005</b>
	<b>Pulsed – Control</b>	<b>1.30</b>	<b>0.49</b>	<b>94</b>	<b>2.66</b>	<b>0.14</b>	<b>2.46</b>	<b>0.024</b>
	Constant – Pulsed	0.26	0.38	94	0.68	-0.65	1.17	0.775

Table 2. The results from pairwise tests of treatment differences in the Estimated Marginal Mean (EMM) number of birds detected at the survey locations within 10 m of the feeders for each species. Estimates of the difference in the EMM and their Standard Errors (SE) are given on the log scale. Comparisons with P-values less than or equal to 0.05 in bold.

<i>Species</i>	<i>Comparison</i>	<i>Estimate</i>	<i>SE</i>	<i>Df</i>	<i>T</i>	<i>Lower CL</i>	<i>Upper CL</i>	<i>P</i>
<b>Chickadee</b>	<b>Constant – Pulsed (Food)</b>	<b>-0.37</b>	<b>0.15</b>	<b>59</b>	<b>-2.52</b>	<b>-0.72</b>	<b>-0.02</b>	<b>0.036</b>
	<b>Constant – Pulsed (No Food)</b>	<b>0.87</b>	<b>0.27</b>	<b>59</b>	<b>3.24</b>	<b>0.23</b>	<b>1.52</b>	<b>0.005</b>
	<b>Pulsed (Food) – Pulsed (No Food)</b>	<b>1.24</b>	<b>0.28</b>	<b>59</b>	<b>4.51</b>	<b>0.59</b>	<b>1.90</b>	<b>&lt;0.001</b>
<b>Titmouse</b>	Constant – Pulsed (Food)	0.42	0.36	60	1.18	-0.43	1.28	0.464
	<b>Constant – Pulsed (No Food)</b>	<b>1.90</b>	<b>0.54</b>	<b>60</b>	<b>3.55</b>	<b>0.62</b>	<b>3.18</b>	<b>0.002</b>
	<b>Pulsed (Food) – Pulsed (No Food)</b>	<b>1.48</b>	<b>0.50</b>	<b>60</b>	<b>2.99</b>	<b>0.30</b>	<b>2.67</b>	<b>0.011</b>
<b>Nuthatch</b>	Constant – Pulsed (Food)	-0.02	0.23	60	-0.07	-0.55	0.52	0.997
	<b>Constant – Pulsed (No Food)</b>	<b>1.74</b>	<b>0.47</b>	<b>60</b>	<b>3.69</b>	<b>0.63</b>	<b>2.86</b>	<b>0.002</b>
	<b>Pulsed (Food) – Pulsed (No Food)</b>	<b>1.76</b>	<b>0.49</b>	<b>60</b>	<b>3.60</b>	<b>0.60</b>	<b>2.92</b>	<b>0.002</b>

Table 3. The results from tests of pairwise treatment effects, comparing the Estimated Marginal Mean (EMM) number of birds detected at point count locations (near and far) for each treatment for each species. Estimates of the differences in the EMM and their standard errors (SE) are given on the log scale. Comparisons with P-values less than or equal to 0.05 in bold.

<i>Species</i>	<i>Treatment</i>	<i>Comparison</i>	<i>Estimate</i>	<i>SE</i>	<i>Df</i>	<i>T</i>	<i>Lower CL</i>	<i>Upper CL</i>	<i>P</i>
<b>Chickadee</b>	<b>Constant</b>	<b>Near - Far</b>	<b>1.67</b>	<b>0.28</b>	<b>124</b>	<b>5.99</b>	<b>1.12</b>	<b>2.22</b>	<b>&lt;0.001</b>
	<b>Pulsed (Food)</b>	<b>Near - Far</b>	<b>2.37</b>	<b>0.43</b>	<b>124</b>	<b>5.57</b>	<b>1.53</b>	<b>3.21</b>	<b>&lt;0.001</b>
	Pulsed (No Food)	Near - Far	0.65	0.45	124	1.45	-0.24	1.54	0.150
<b>Titmouse</b>	<b>Constant</b>	<b>Near - Far</b>	<b>1.62</b>	<b>0.31</b>	<b>125</b>	<b>5.23</b>	<b>1.01</b>	<b>2.24</b>	<b>&lt;0.001</b>
	<b>Pulsed (Food)</b>	<b>Near - Far</b>	<b>2.42</b>	<b>0.75</b>	<b>125</b>	<b>3.24</b>	<b>0.94</b>	<b>3.89</b>	<b>0.002</b>
	Pulsed (No Food)	Near - Far	0.28	0.69	125	0.41	-1.08	1.64	0.686
<b>Nuthatch</b>	<b>Constant</b>	<b>Near - Far</b>	<b>2.03</b>	<b>0.38</b>	<b>125</b>	<b>5.40</b>	<b>1.29</b>	<b>2.78</b>	<b>&lt;0.001</b>
	<b>Pulsed (Food)</b>	<b>Near - Far</b>	<b>2.75</b>	<b>0.73</b>	<b>125</b>	<b>3.77</b>	<b>1.30</b>	<b>4.19</b>	<b>&lt;0.001</b>
	Pulsed (No Food)	Near - Far	-0.28	0.59	125	-0.48	-1.44	0.88	0.633

Table 4. The results from pairwise statistical comparisons of treatment effects on the number of birds detected at point count locations (near and far); presented are the differences in Estimated Marginal Mean (EMM) number of birds. For example, the difference in the number of birds near and far from feeders with constant access is compared to the difference in the number of birds near and far from feeders with pulsed access with no food available. Estimates of the “difference of differences” in the EMM and their standard errors (SE) are given on the log scale. Comparisons with P-values less than or equal to 0.05 in bold.

<i>Species</i>	<i>Comparison</i>	<i>Estimate</i>	<i>SE</i>	<i>Df</i>	<i>T</i>	<i>Lower CL</i>	<i>Upper CL</i>	<i>P</i>
<b>Chickadee</b>	Pulsed (Food) – Constant	0.70	0.51	124	1.37	-0.51	1.91	0.358
	Constant – Pulsed (No Food)	1.02	0.53	124	1.94	-0.23	2.27	0.1312
	<b>Pulsed (Food) – Pulsed (No Food)</b>	<b>1.72</b>	<b>0.62</b>	<b>124</b>	<b>2.79</b>	<b>0.26</b>	<b>3.18</b>	<b>0.017</b>
<b>Titmouse</b>	Pulsed (Food) – Constant	0.79	0.80	125	0.99	-1.10	2.69	0.581
	Constant – Pulsed (No Food)	1.35	0.75	125	1.80	-0.43	3.12	0.174
	Pulsed (Food) – Pulsed (No Food)	2.14	1.01	125	2.11	-0.25	4.53	0.089
<b>Nuthatch</b>	Pulsed (Food) – Constant	0.71	0.82	125	0.87	-1.22	2.65	0.656
	<b>Constant – Pulsed (No Food)</b>	<b>2.31</b>	<b>0.70</b>	<b>125</b>	<b>3.32</b>	<b>0.67</b>	<b>3.96</b>	<b>0.003</b>
	<b>Pulsed (Food) – Pulsed (No Food)</b>	<b>3.03</b>	<b>0.94</b>	<b>125</b>	<b>3.24</b>	<b>0.82</b>	<b>5.24</b>	<b>0.004</b>

Table 5. The results from pairwise treatment comparisons of slopes in treatment  $\times$  Julian date interactions; presented are the differences in the Estimated Marginal Mean (EMM) slopes for pair of treatments. Estimates of the Difference in the EMM slopes and their standard errors (SE) are given on the log scale. Comparisons with P-values less than or equal to 0.05 in bold

<i>Species</i>	<i>Comparison</i>	<i>Estimate</i>	<i>SE</i>	<i>Df</i>	<i>T</i>	<i>Lower CL</i>	<i>Upper CL</i>	<i>P</i>
<b>Chickadee</b>	Constant – Pulsed (Food)	0.13	0.15	57	0.87	-0.23	0.50	0.654
	<b>Constant – Pulsed (No Food)</b>	<b>-0.72</b>	<b>0.27</b>	<b>57</b>	<b>-2.73</b>	<b>-1.36</b>	<b>-0.09</b>	<b>0.021</b>
	<b>Pulsed (Food) – Pulsed (No Food)</b>	<b>-0.86</b>	<b>0.27</b>	<b>57</b>	<b>-3.13</b>	<b>-1.51</b>	<b>-0.20</b>	<b>0.007</b>
<b>Titmouse</b>	Constant – Pulsed (Food)	-0.17	0.24	58	-0.70	-0.72	0.39	0.746
	Constant – Pulsed (No Food)	-2.53	1.14	58	-2.22	-5.19	0.13	0.064
	Pulsed (Food) – Pulsed (No Food)	-2.37	1.15	58	-2.06	-5.05	0.31	0.093
<b>Nuthatch</b>	Constant – Pulsed (Food)	0.17	0.23	58	0.73	-0.38	0.71	0.728
	Constant – Pulsed (No Food)	-2.20	1.00	58	-2.20	-4.53	0.13	0.068
	<b>Pulsed (Food) – Pulsed (No Food)</b>	<b>-2.37</b>	<b>1.01</b>	<b>58</b>	<b>-2.36</b>	<b>-4.72</b>	<b>-0.02</b>	<b>0.048</b>

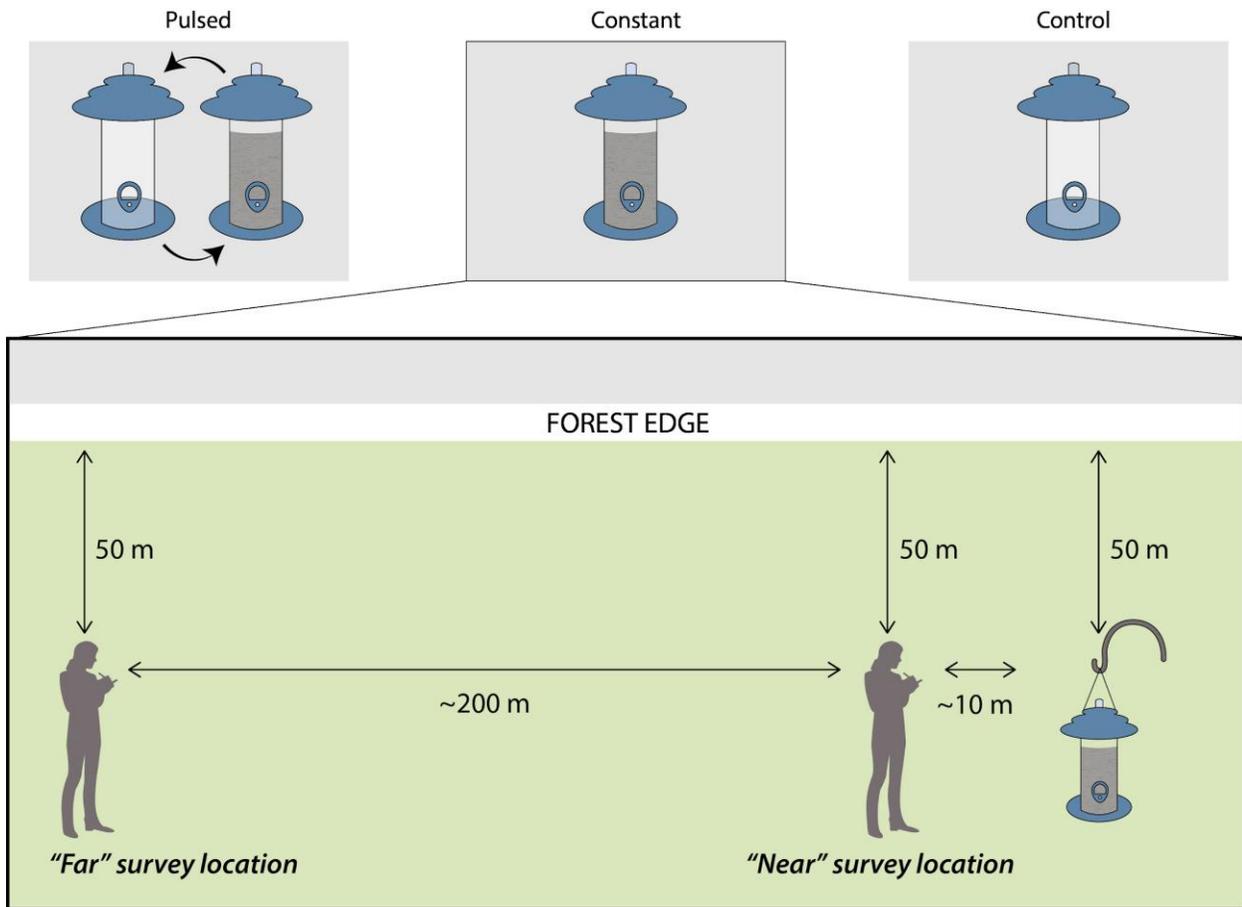


Figure 1. A schematic of the study design depicting one of the three replicate groups. There were three sites each with one treatment: pulsed access, constant access, and control (no) access to supplemental food. For each site there were two survey points, located ~10 m and ~200 m from the feeder at each site. All survey points are placed ~50 m from the forest edge. In the schematic, shaded feeders indicate that supplemental food is available and unshaded feeders indicate that supplemental food is unavailable. Graphic by Jillian Ditner.

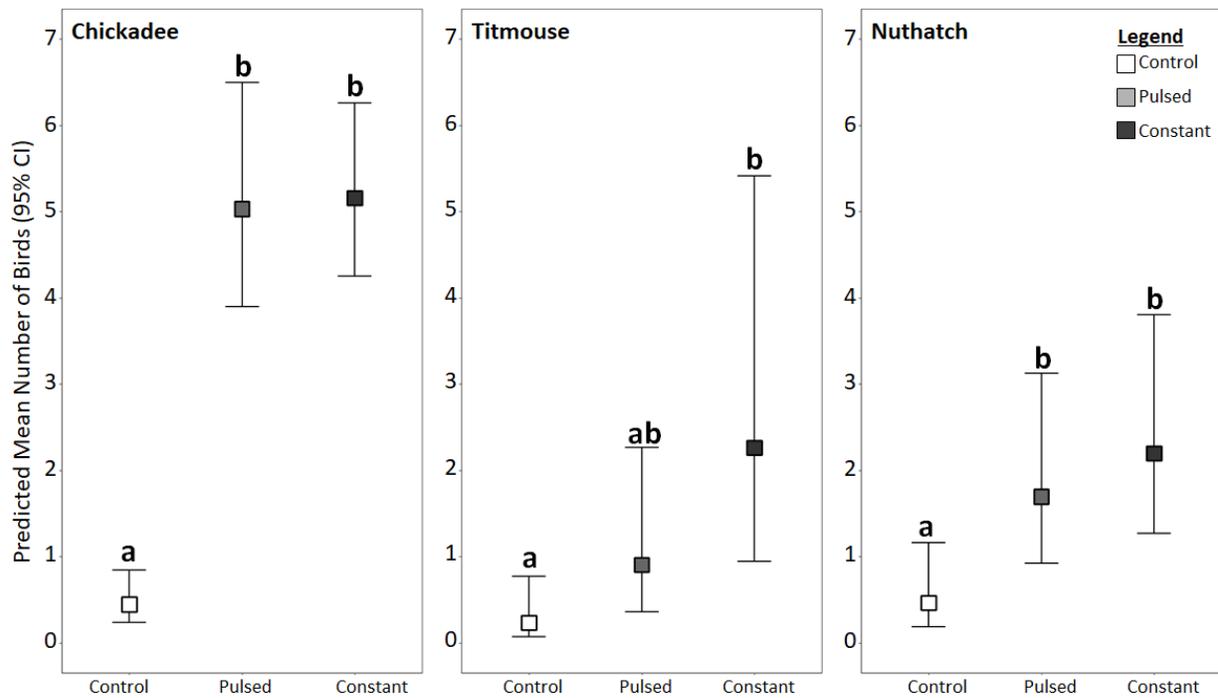


Figure 2. The Estimated Marginal Mean (EMM) number of birds detected at a site (near and far survey locations combined) for each supplementation treatment, with 95% confidence intervals on the response scale. Differences in letters indicate a statistically significant ( $P < 0.05$ ) difference between treatments.

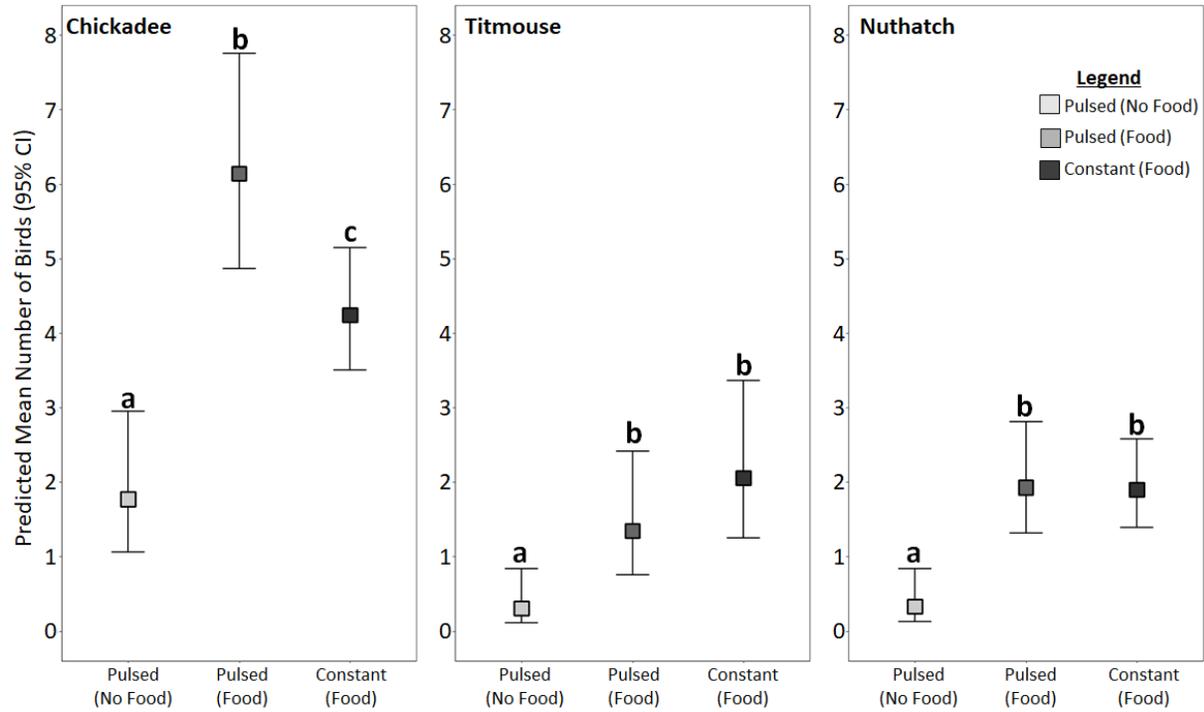


Figure 3. The Estimated Marginal Mean (EMM) number of birds detected within ~10 m of supplemental feeders with 95% confidence intervals on the response scale for each supplemental food treatment. Differences in letters indicate a statistically significant ( $P < 0.05$ ) difference between treatments.

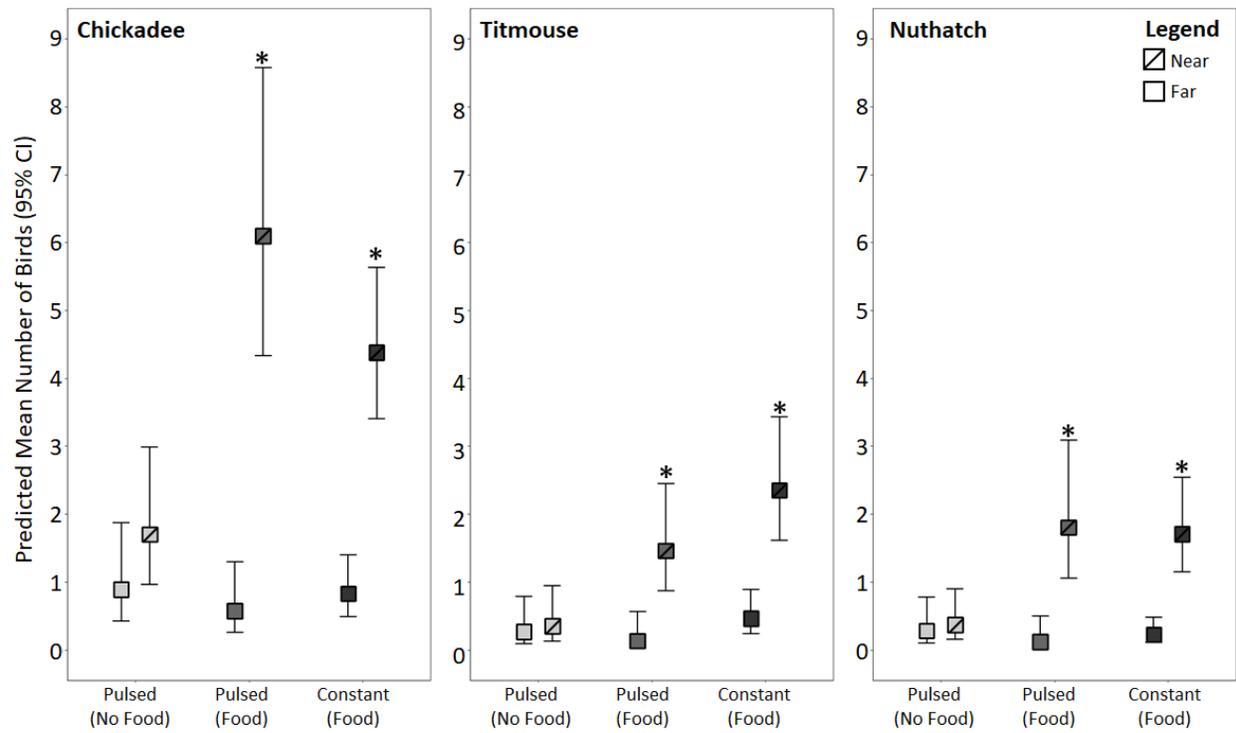


Figure 4. The Estimated Marginal Mean (EMM) number of birds detected at survey points located near (within 10 m) and far (~ 200 m) from feeders. Data show 95% confidence intervals on the response scale for each survey location within each treatment. The \* indicates a statistically significant ( $P < 0.05$ ) difference between near and far locations within a treatment.

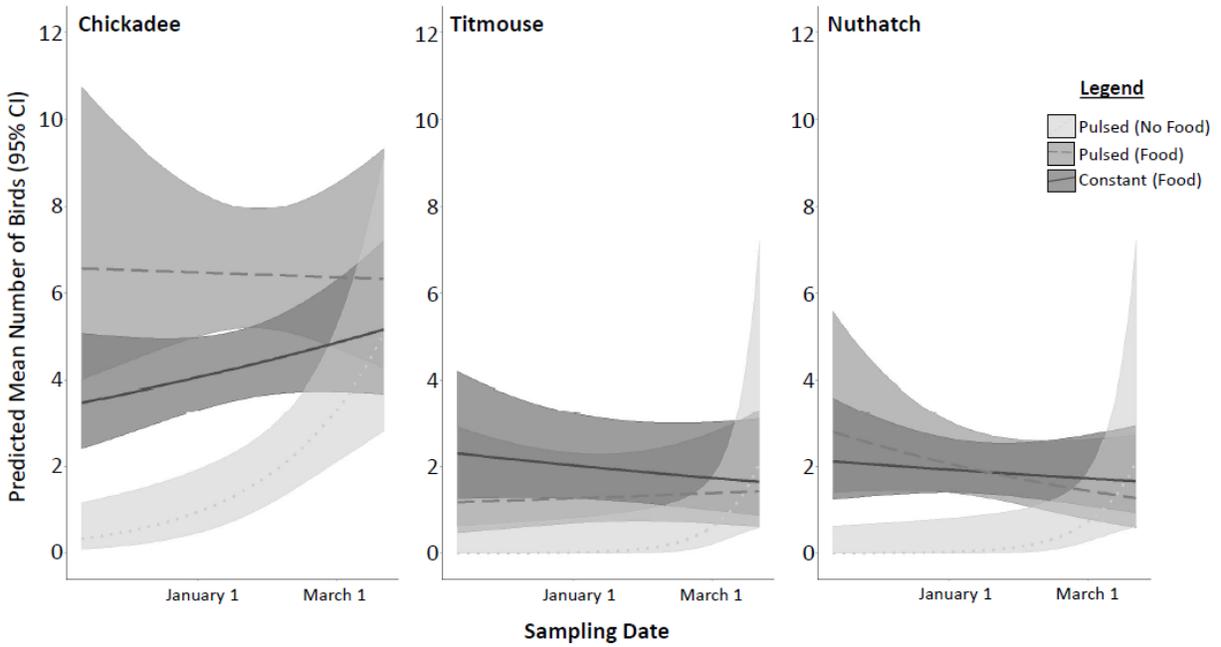


Figure 5. Seasonal changes in the Estimated Marginal Mean (EMM) number of birds seen near feeders (10 m) as the winter season advances. Shading indicates 95% confidence bands on the response scale for each supplemental food.