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Article

Experimentally induced flight costs do not lead to increased reliance on supplemental food in winter by a small songbird

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Each year hundreds of millions of people intentionally feed wild animals throughout the world. For decades, concerns have persisted regarding the potential for intentional feeding to promote dependency on human-supplemented food, particularly during energetically demanding periods of the annual cycle. In this study, we evaluated whether individuals subjected to experimentally increased flight costs responded by increasing their use of supplemental feeders in a wild, free-ranging population of the black-capped chickadee *Poecile atricapillus*. We subjected 67 RFID-tagged chickadees to one of three handicapping treatments (heavy feather-clipping, light feather-clipping or unclipped controls) and then evaluated feeder use of each individual relative to their pre-treatment level. Contrary to predictions, we found that chickadees in both feather-clipping treatments exhibited a short-term reduction in feeder use, returning to feeding levels of unmanipulated controls within approximately two weeks of treatment implementation. Similarly, experimental feather-clipping treatments had little influence on changes in the number of feeders used or on the timing of feeder visits across the daily cycle, relative to controls. Our results indicate that experimental handicapping of chickadees led to relatively minor and transient changes in the use of supplemental food with no evidence that handicapped individuals increased their reliance on supplemental bird feeders. These findings suggest that recreational bird feeding is unlikely to lead to feeder dependency in small songbirds during winter, although additional research on this topic should be a priority given the global footprint of intentional feeding of wildlife.

Keywords: bird feeding, black-capped chickadee, experimental handicapping, feather clipping, *Poecile atricapillus*, supplemental feeding

Introduction

Intentional feeding of wildlife by humans is a widespread activity that occurs throughout the world and supports a multi-billion dollar global industry (Baicich et al. 2015, Cox and Gaston 2018, Jones 2018). For example, more than 50 million people in the United States provide supplemental food for birds, with more than US\$4 billion spent annually on bird food, feeders and accessories (USFWS 2011, Baicich et al.



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2015); similar patterns of bird feeding are found throughout other parts of the world, including the United Kingdom and Australia (Ishigame and Baxter 2007, Davies et al. 2012, Reynolds et al. 2017). The extensive and widespread nature of intentional feeding has a range of consequences for wild, free-ranging animal populations, which are best-documented in birds. These include negative effects such as facilitating disease transmission (Adelman et al. 2015, Becker et al. 2015, Cox and Gaston 2018), enhancing competition (Rickett et al. 2013), impairing breeding performance (Plummer et al. 2013a, b, Malpass et al. 2017) and restructuring local communities (Galbraith et al. 2015), as well as positive effects that include enhanced winter survival (Brittingham and Temple 1988, Danner et al. 2013), body condition (Desrochers and Turcotte 2008, Wilcoxon et al. 2015, Broggi et al. 2021) and reproductive output (Robb et al. 2008a). Furthermore, intentional feeding of wild bird populations has been found to result in changes to migration behavior (Plummer et al. 2015), bill structure (Bosse et al. 2017) and even the structure of gametes (Stostad et al. 2019), suggesting that supplemental feeding may impact wild animal populations in ways that are not fully understood at the current time.

As more is learned about how wild bird populations are impacted by intentional supplemental feeding, discussion around whether such practices should be regulated has led some countries to establish policies and best management practices regarding supplemental feeding of wildlife (Reynolds et al. 2017, Baverstock et al. 2019). Central to arguments on both sides of this debate is whether intentional human feeding results in wild, free-ranging populations becoming reliant on human-supplemented food (Reynolds et al. 2017). This concern is especially relevant to bird feeding in northern latitudes during winter – when ambient temperatures are the lowest and the extent of daylight for foraging is shortest – because bird feeding is commonly practiced in these regions, and motivations for supplemental feeding are often focused on helping birds survive during energetically demanding periods, such as cold weather and winter storms (Baicich et al. 2015, Reynolds et al. 2017, Jones 2018). Nevertheless, very few studies have experimentally evaluated whether free-ranging birds increase their reliance upon supplemental food sources during energetically demanding periods, despite its importance for informing the debate about whether policies should be enacted to regulate intentional feeding practices (Jones and Reynolds 2008, Robb et al. 2008b). The lone manipulative experiment to test this idea examined winter survival of the black-capped chickadee (*Poecile atricapillus*, hereafter chickadee) using supplemental feeders and found no reductions in apparent survival after removal of bird feeders that had provided supplemental food in winter for 25 years, leading to the conclusion that bird feeding did not promote feeder dependency (Brittingham and Temple 1992). This remains the only study that has used an experimental approach to test for feeder dependence, so much remains to be learned about the degree to which wild, free-ranging birds increase their reliance on supplemental food, especially during energetically demanding periods of the annual cycle.

In this study, we evaluated whether individuals experiencing experimentally increased flight costs altered their use of supplemental bird feeders during winter using bird feeders equipped to detect radio-frequency identification (RFID) tags (Bonter and Bridge 2011). We experimentally removed primary flight feathers from chickadees at two different intensities (i.e. light and heavy feather-clipping treatments; Rivers et al. 2017) and then compared their post-treatment use of supplemental feeders to that of unclipped control birds. Experimental removal of primary feathers is a well-known technique that alters wing-loading and increases the energetic cost of initiating and maintaining flight (Pennycuik 1989, Swaddle and Witter 1997, Lind and Jakobsson 2001, Carrascal and Polo 2006). Thus, we used feather clipping to impose energetic challenges that would be expected to induce behavioral changes in treated birds related to their use of supplemental feeders. Furthermore, we assumed that chickadees subjected to feather-clipping would require more energy to maintain the same activity levels as unclipped control birds, and the amount of energy required for a given activity level would be greater for individuals undergoing the heavy feather-clipping treatment relative to the light feather-clipping treatment. We predicted that, relative to unclipped controls whose feathers remained intact, individual birds that experienced feather-clipping treatments would increase feeder visitation rates to maximize foraging efficiency and reduce foraging costs incurred when selecting natural foods (Reynolds et al. 2017), with visitation rates being greater for birds in the more intensive feather-clipping treatment. In addition, we predicted that the number of supplemental feeders used by chickadees would be greatest in control birds and decrease with the intensity of feather clipping to minimize movement costs (Swaddle and Witter 1997, Carrascal and Polo 2006). Finally, we measured the timing of feeder visits across the daily cycle, and predicted that, on average, individuals undergoing the heaviest clipping treatment would arrive at feeders earliest in the day followed by birds in the light clipping treatment and then the control treatment, as a shift to earlier feeder visits would be expected for small birds in winter like the chickadee whose energetic reserves are predicted to be lowest in the morning after expending energetic reserves overnight (Lima 1986, McNamara et al. 1994, Brodin 2007, Bonter et al. 2013). As an alternative, we also tested whether handicapping led to a reduction in the use of supplemental feeders, as it is possible that feather-clipped individuals would avoid bird feeders after treatments were implemented because removing flight feathers can reduce lift and take-off speed and, in turn, lead to increased predation risk at bird feeders (Swaddle et al. 1999, Kullberg and Lafrenz 2007) where songbirds may be more prone to attack by avian predators (Dunn and Tessaglia 1994, Kullberg et al. 1998). Under this alternative scenario, feather-clipped birds were predicted to decrease their use of supplemental bird feeders relative to unclipped individuals, with the degree of feeder use decreasing with the intensity of feather clipping. In addition, feather-clipped birds would also be expected to use fewer feeders than control birds and not show changes in the timing of feeder visits during the day.

Methods

Study area and RFID-equipped feeding stations

We conducted this study from 23 October 2016 until 1 April 2017 along the Oak Creek riparian zone near the campus of Oregon State University in Corvallis, Oregon, USA (44.6°N, 123.3°W, 90 m a.s.l.). Vegetation cover was similar among bird feeder locations and was dominated by willow (*Salix* spp.), poplar (*Populus* spp.), white alder (*Alnus rhombifolia*), Oregon white oak (*Quercus garryana*), bigleaf maple (*Acer macrophyllum*) and Himalayan blackberry (*Rubus discolor*; Lajoie 2018). We selected the chickadee for our study because it is a small songbird (10–14 g, Smith 1991, Lajoie et al. 2019) that frequents bird feeders during winter throughout its range, has a high surface area to volume ratio with high mass-specific metabolic rates, has high daily energy requirements (Kessel 1976, Smith 1991, Karasov et al. 1992, Petit and Vezina 2014), and typically takes one seed at a time during each feeder visit and which allows for a clear measure of feeder visitation rate. Thus, it is an ideal species for evaluating how energetic challenges lead to behavioral changes in feeder use during winter (Kessel 1976, Lima 1985, Brittingham and Temple 1992). It should be noted that the chickadee, like other members of the family Paridae, exhibit food-caching behavior, which can include sunflower seeds obtained from supplemental bird feeders (Lima 1985, Barnea and Nottebohm 1995). This behavior increases markedly during autumn and declines in early winter (Sherry 1989, Brodin 2005, Hoshoooley et al. 2007) with some evidence of food-storing in spring; nevertheless, this remains a poorly studied component of chickadee feeding behavior (Pravosudov 2006, 2007).

We placed 21 bird feeders in our study area, with 3.2 km separating the two most distant feeders; feeders were approximately 200 m apart except in one location where we placed a feeder approximately 400 m away from the next nearest feeder because of restricted land access (Lajoie 2018). Residential housing density was low in our study area, and although it is possible that birds in our study used residential bird feeders that were not part of our study, our treatment randomization (described below) should have resulted in all treatment groups having equal access to any residential feeders that may have been present. Thus, any influence of residential feeders on our RFID-tagged birds – if such influence was indeed present – would not lead to any systematic bias and instead would have only introduced random noise into our measurements of feeder use. To quantify feeder visits, we built customized PVC tube feeders that held approximately 3 kg of black oil sunflower seed (Global Harvest Foods Limited, Seattle, Washington, USA) and were equipped with an RFID data logger. The data logger was set to record feeder visits during daylight hours (i.e. 1 h before sunrise until 1 h after sunset) and was attached to a customized RFID antenna that served as a perch for birds accessing the single seed access port; thus, each feeder accommodated one bird at a time which allowed for clearly delineating feeder visits by tagged birds (Bonter and Bridge 2011). We created RFID antennae

by tightly coiling magnet wire into an oval shape (Bridge and Bonter 2011, Turner et al. 2020), and we found that optimal antenna inductance was achieved by approximately 102 turns of the antenna wire. We dipped all antennae in a durable rubber coating to ensure weather-proofing and conductance and then attached them to feeders by zip-tying the coated antenna to a single plastic feeder port perch and two 7.6 cm Deckmate coated metal screws (Fig. 1). Although Bridge and Bonter (2011) reported that RFID communication can be impeded by large metal objects, we found no evidence that the ability of our readers to correctly read tags was compromised by the use of metal screws through testing that we implemented regularly (below).

Each RFID data logger recorded the date, time of day (to the nearest second), unique bird identification number and feeder identification number on a memory storage card. We downloaded data from each feeder's data logger regularly throughout the course of our study, and our procedure included using an RFID 'test tag' to validate the functionality of the RFID system after data were downloaded. We used this testing procedure on every feeder after each data download event totaling > 350 occasions, and in all cases we found that the RFID readers correctly read the test tag. For our investigation we considered a 'feeder visit' to be an RFID-logged visit at a feeder that was separated from any previous visit by the same individual by at least 10 s. We used this criteria because chickadees typically take > 10 s to handle sunflower seeds that are obtained from feeders (Lima 1985), including in our study area (Lajoie 2018), and because the sampling rate for the logger was set to capture short feeder visits (< 1 s) and separating visits by 10 s avoided double-counting the same chickadee during single feeder visits. Because chickadees obtain a single sunflower seed during most bird feeder visits (Ficken et al. 1990), we assumed that each feeder visit by an individual bird resulted in the removal of a single sunflower seed, although we were unable to determine if seeds removed from feeders were consumed immediately or cached for future use.

Sunflower seeds were available to birds ad libitum in all feeders starting approximately four weeks prior to the start of this study (i.e. 24 September 2016) through to the time when the study ended (i.e. 1 April 2017). Although we were unable to prevent other species from using RFID-equipped feeders, it is unlikely that feeder use by other species prevented tagged chickadees from visiting feeders, for two reasons. First, our feeders held 3 kg of sunflower seed and were refilled regularly so that each feeder provided ad libitum food throughout the entire course of our study. Second, we recorded > 325 000 visits by chickadees over the course of the winter – an average of > 4800 visits/bird – and such a high visitation rate would not be feasible if chickadees were prevented from using feeders by other species.

Chickadee capture and tagging

Birds in this study comprised $n=88$ chickadees banded in fall 2016 with an additional $n=86$ chickadees banded during

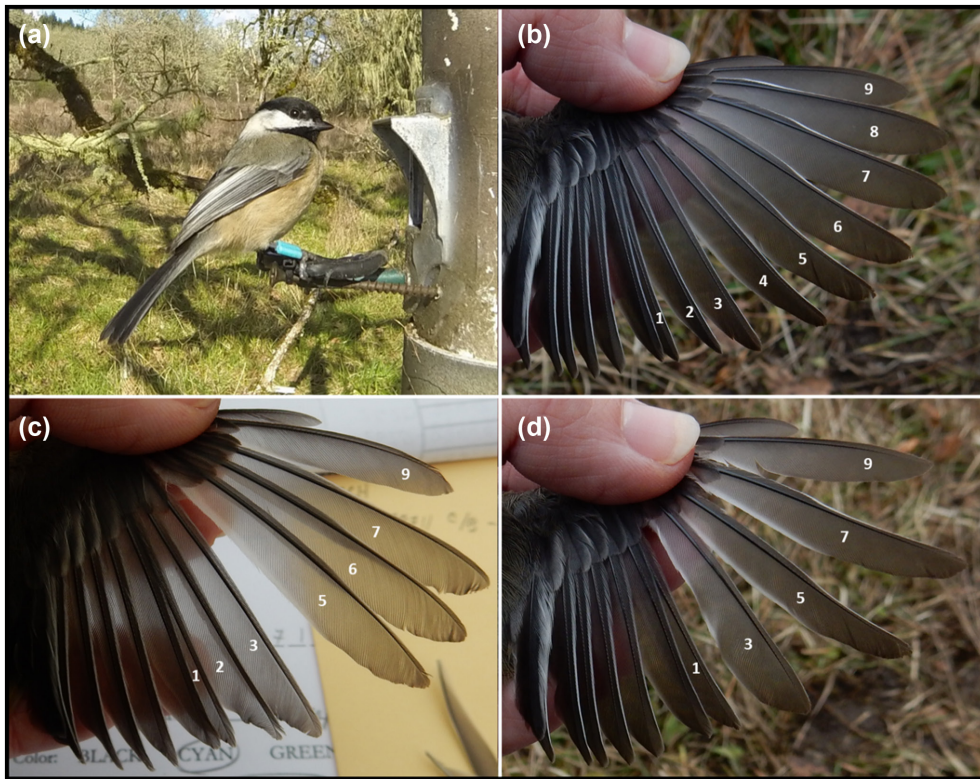


Figure 1. (a) A banded black-capped chickadee during a feeder visit illustrating the PIT tag (light blue band on right leg) that allowed for quantifying feeder visits and testing the extent to which handicapped birds relied on supplemental feeders. Each chickadee was randomly assigned to one of three treatments: (b) unclipped control treatment, where no primary flight feathers were removed, (c) light feather-clipping treatment, where two primary feathers were removed from each wing and (d) heavy feather-clipping treatment, where four primary feathers were removed from each wing. The numbers superimposed on primary feathers indicate intact feathers that remained following the implementation of each treatment.

pilot work in the previous winter (December 2015–February 2016). We captured birds with mist nets and/or on-feeder traps and fitted them with a colored polypropylene leg band embedded with a uniquely numbered passive integrated transponder (PIT) tag (IB Technology, Aylesbury, UK), a uniquely numbered U.S. Geological Survey aluminum band, and up to two colored plastic leg bands to allow for individual identification. We also recorded body mass, right tarsus length and flattened right wing chord for each individual at its initial capture; body mass was again measured at the time when treatments were applied to each bird which allowed us to compare body mass of birds assigned to different treatments. Given extensive individual variation in feeder use by unmanipulated chickadees in our study system (Lajoie et al. 2019), we began recording feeder visitation data in January 2017 to obtain pre-treatment data that allowed us to control for individual differences in feeder use. Following this pre-treatment period we conducted trapping sessions at all feeders across a five-week period (25 January–2 March 2017) to recapture as many previously banded chickadees as possible. A total of $n=68$ birds were recaptured and available for this study; this included 19 of the 86 birds that were banded in the pilot season and 49 of the 88 birds banded in fall 2016; the smaller proportion of handicapped birds from

the pilot study is likely due to mortality and/or emigration from the study area. Of note, we only used birds that served as unclipped controls during our pilot season so that no birds in this study experienced feather clipping more than once.

Upon recapture, we applied one of our three treatments to each chickadee, regardless of when it was originally captured (i.e. unclipped control, light feather-clipping or heavy feather-clipping; Fig. 1). Thus, each treatment was randomly allocated to one individual for every three chickadees that were caught in succession. We attempted to trap birds at all feeders to ensure even representation of the three treatments through time and across feeding locations. In the light feather-clipping treatment we removed two flight feathers from each wing (i.e. primary 4 and 8; 22% of primary feathers; $n=23$ individuals) whereas in the heavy feather-clipping treatment we removed four flight feathers from each wing (i.e. primary 2, 4, 6 and 8; 44% of primary feathers; $n=23$ individuals; Fig. 1). We clipped feathers at their base with a pair of sharp scissors so that they did not regrow during the course of our study, ensuring that birds were exposed to functional feather loss alone and did not incur physiological costs arising from feather regeneration during the post-treatment period. We handled individuals in the unclipped control group ($n=22$ individuals) identically to individuals

whose feathers were clipped, except that we removed none of their feathers. All procedures described were conducted under permits approved by Oregon State University, the Oregon Department of Fish and Wildlife and the U.S. Geological Survey.

Quantifying use of RFID-equipped feeders

Our study required a balance between 1) obtaining adequate pre-treatment feeder visitation data that provided information on the 'baseline' feeding rate for each individual under study, and 2) obtaining adequate post-treatment feeder visitation data that provided a reasonable chance of detecting treatment effects. We opted for this approach because our previous work found that individual variation in feeder use by chickadees in our system was extensive (Lajoie et al. 2019) and thus made it imperative that we collected pre-treatment data to control for individual differences. Ultimately, these requirements reduced the window of time for monitoring birds during the winter season, and we elected to put more time towards monitoring post-treatment effects than towards establishing baseline feeding patterns for each individual. We also constructed time periods a priori so they were short enough to detect rapid effects after treatments were applied because small songbirds can exhibit rapid physiological responses to feather-clipping in as little as a week following treatment (Lind and Jakobsson 2001, Kullberg et al. 2002a). Therefore, for each PIT-tagged bird we summarized the number of visits per day for each of five time periods: 1–20 days prior to treatment application, 1–5 days post-treatment, 6–10 days post-treatment, 11–20 days post-treatment and 21–30 days post-treatment. For each individual and during each period we initially calculated the average daily visits by summing the number of visits made to all feeders and then dividing it by the number of days in the period. We then took the average daily visit value from the pre-treatment period and subtracted it from each of the average daily visit values for the four post-treatment periods to control for variation among individuals (Lajoie et al. 2019); we refer to each of these resulting values as the 'adjusted daily feeder visitation rate.' Similarly, we summed the number of different RFID-equipped feeders used by each bird in each period and then subtracted the number of feeders used during the pre-treatment period from the number of feeders used in each of the post-treatment periods; we refer to this as the 'adjusted number of feeders used.' Finally, we identified the hour relative to sunrise during which each feeder visit occurred to evaluate whether birds in feather-clipping treatments shifted the time of their visits. We obtained sunrise and sunset times for the Corvallis Municipal Airport in Corvallis, Oregon, USA (44°33'N, 123°15'W) from the Global Monitoring Laboratory of the National Oceanic and Atmospheric Administration (NOAA 2021) In each of the four post-treatment periods, we summed the number of visits each bird made to all feeders in four post-sunrise bins, each 2 h in length: up to 2, 4–5, 7–8 and 10–11 h post-sunrise; we refer to this response as the 'hourly visitation rate.'

Statistical analysis

We constructed linear mixed models in the R statistical environment for all of our analyses (v4.0.2; <www.r-project.org>). To evaluate the effects of feather-clipping treatments on feeder use we used the 'nlme' package (ver. 3.1-131; Pinheiro et al. 2021) to construct a model with a normal distribution that contained adjusted daily feeder visitation rate as the response variable, handicapping treatment (3 levels) and post-treatment time period (4 levels) as fixed effects, and individual bird identity as a random effect. In addition, we used the same model structure to evaluate how feather-clipping treatments influence the adjusted number of feeders used. Because of the potential for temporal autocorrelation between time periods, we evaluated four different models of the correlation structure among time periods for each response variable and use Akaike's information criterion (AIC) to determine the correlation structure with the most support. The autoregressive order one correlation structure was best supported for the mean adjusted daily visitation rate and therefore used in subsequent analyses. In contrast, the general correlation structure was best supported for the mean adjusted number of feeders used, which allowed for different correlations between each pair of time periods, was used in subsequent analyses.

To evaluate the relationship between feather-clipping treatments and the timing of feeder visits during the day we used the 'glmmTMB' package (Magnusson et al. 2020) to construct a model with a Poisson distribution and a logarithmic link function, using hourly visitation rate as the response variable, with handicapping treatment (3 levels) and daily time period (4 levels) as fixed effects, and individual bird identity as a random effect. For each period we fit five models of differing complexity to evaluate evidence for treatment and daily time period effects (Table 1). The first model was the most complex and allowed the interaction of treatment and hour since sunrise, the second model included only main effects of treatment and sunrise, the third included only the main effect of treatment, the fourth included only the effect of hour since sunrise and the fifth did not allow the mean to vary (Table 1). We used AIC statistics to identify the best supported model for each post-treatment time period (Burnham and Anderson 2004). AIC is a relative measure of model support with small AIC values indicating greater data support for a model compared to another model. For each period we identified the model with the smallest AIC value and calculated the change in AIC (Δ AIC) between each of the remaining four models and the model with the smallest AIC. We considered a Δ AIC of less than five to indicate two models with roughly similar support; however, we used the most complex model to estimate effects in keeping with current guidance on the use of p-values (Wasserstein and Lazar 2016). Similar to our other analysis modeling temporal autocorrelation, we used AIC statistics to identify the best-supported autocorrelation structure.

For all models, distributional assumptions were upheld based on visual assessment of scatter plots of the normalized

Table 1. Model selection results from candidate models describing the effects of experimental feather-clipping treatments and time of day on mean hourly feeder visits during four post-treatment periods. Models are ranked in ascending order of the change in Akaike's information criterion (Δ AIC) between the best supported model and all other models.

Model set/model description	K^a	Δ AIC	w_i^b	ER ^c
Post-treatment period 1				
Hours since sunrise (HSS)	4	0.00 ^d	0.60	1.0
Main effects model (HSS+TRT)	6	2.10	0.21	2.9
Null model	1	3.34	0.11	5.3
Full model (HSS+TRT+HSS \times TRT)	12	5.33	0.04	14.4
Treatment effects model (TRT)	3	5.73	0.03	17.5
Post-treatment period 2				
Main effects model (HSS+TRT)	6	0.00 ^e	0.79	1.0
Hours since sunrise (HSS)	4	2.98	0.18	4.4
Full model (HSS+TRT+HSS \times TRT)	12	6.60	0.03	27.1
Treatment effects model (TRT)	3	11.26	< 0.01	278.7
Null model	1	13.72	< 0.01	953.4
Post-treatment period 3				
Main effects model (HSS+TRT)	6	0.00 ^f	0.68	1.0
Hours since sunrise (HSS)	4	1.66	0.29	2.3
Full model (HSS+TRT+HSS \times TRT)	12	6.28	0.03	23.1
Treatment effects model (TRT)	3	20.43	< 0.01	27 309.8
Null model	1	22.46	< 0.01	75 357.6
Post-treatment period 4				
Main effects model (HSS+TRT)	6	0.00 ^g	0.58	1.0
Hours since sunrise (HSS)	4	0.66	0.41	1.4
Full model (HSS+TRT+HSS \times TRT)	12	8.30	0.01	63.4
Treatment effects model (TRT)	3	25.87	< 0.01	414 571.2 562 417.6
Null model	1	26.48	< 0.01	

^a Denotes number of fixed effects parameters in model.

^b Relative likelihood of the current model (i) based on AIC value.

^c Evidence ratio.

^d Top-ranking model for period 1: AIC=1212.00.

^e Top-ranking model for period 2: AIC=1413.35.

^f Top-ranking model for period 3: AIC=1654.46.

^g Top-ranking model for period 4: AIC=1732.25.

residuals plotted against fitted values and a normal quantile-quantile plot. We compared the estimated mean adjusted daily visitation rate and estimated adjusted number of feeders used between the unclipped control group and the light feather-clipping group, and between the unclipped control group and the heavy feather-clipping group for each period. We adjusted the 95% confidence intervals (CIs) using the Dunnett's correction for multiple tests when evaluating

hourly visitation rate and number of feeders used. We used an alpha of 0.05 for statistical tests and interpreted $p < 0.04$ as evidence of a statistical difference, $p = 0.04-0.06$ as some evidence of statistical difference and $p > 0.06$ as no evidence of statistical difference.

Results

Pre-treatment measurements of chickadees and feeder use

We detected no differences between the average size of chickadees in the three treatment groups as measured by body mass ($F_{2,62} = 0.95$, $p = 0.393$), right tarsus length ($F_{2,64} = 0.95$, $p = 0.393$) or flattened right wing chord ($F_{2,64} = 0.38$, $p = 0.689$) prior to treatment implementation. We also detected no differences among the three treatment groups in the average daily feeder visitation rate in the 20-day period immediately prior to when we implemented treatments (control: 28.0 visits [SD=25.4], light clipping: 23.8 visits [SD=21.4], heavy clipping: 26.0 visits [SD=26.1]; $F_{2,64} = 0.17$, $p = 0.845$). Similarly, we detected no differences in the average number of feeders used between birds in the three treatment groups during the pre-treatment period (control: 1.8 feeders [SD=0.69], light clipping: 1.9 feeders [SD=1.11], heavy clipping: 1.8 feeders [SD=0.78]; $F_{2,64} = 0.14$, $p = 0.873$). Finally, during the pre-treatment period we detected similar average mean hourly visitation rate for each of the daily time periods among individuals in the three treatment groups. Thus, chickadees in all three treatment groups were similar in their physical size and their use of supplemental feeders immediately prior to when we implemented feather-clipping treatments.

Post-treatment feeder use

Sixty-seven of the 68 individuals (98.5%) that were recaptured and assigned to a treatment group ultimately returned to at least one feeder after treatments were implemented. The lone bird that did not return experienced the light feather-clipping treatment and its reason for not returning was unknown; nevertheless, this individual was removed from all subsequent analyses. After treatments were implemented, individuals in the control group returned to feeders fastest, followed by individuals in the light feather-clipping treatment, and then those in the heavy feather-clipping treatment (Fig. 2); collectively, > 88% of the chickadees used in our study returned to a feeder within seven days of treatment implementation.

We found no evidence that the differences in mean adjusted daily feeder visitation rates among the post-treatment periods were strongly influenced by feather-clipping treatments ($F_{7,15} = 8.30$, $p = 0.217$). Mean daily visitation rates were consistently higher for individuals in the light feather-clipping treatment relative to the heavy feather-clipping treatment for all post-treatment periods (Fig. 3a). The estimated mean adjusted daily visitation rate for individuals in both feather-clipping groups decreased relative

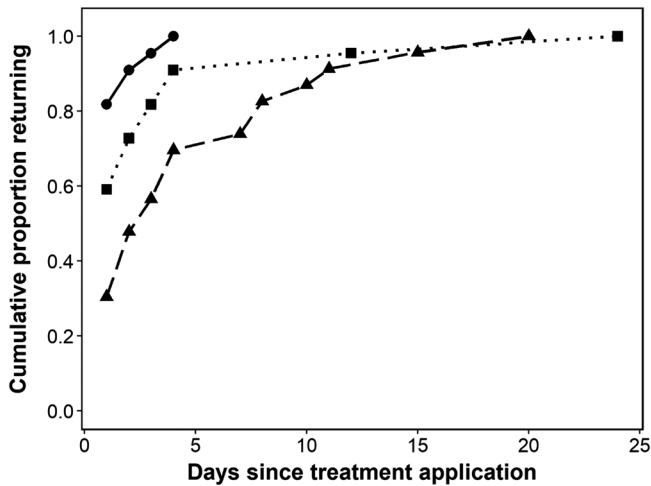


Figure 2. The cumulative proportion of individual chickadees in each treatment group that returned to RFID-equipped bird feeders as a function of time since feather-clipping treatments were implemented. A single individual in the light feather-clipping treatment group did not return to feeders after treatments were implemented and was excluded from all analyses. Note that all chickadees in the control group (filled circles, solid lines) returned shortly after treatment application and thus reached a cumulative proportion of one within four days of treatment application, whereas the return of all chickadees to a feeder in both the light feather-clipping treatment (filled squares, dotted lines) and the heavy feather-clipping treatment (filled triangles, dashed lines) took longer. Final sample sizes were $n=22$ for the control group, $n=22$ for the light feather-clipping treatment and $n=23$ for the heavy feather-clipping treatment.

to controls in the first (1–5 days) and second (6–10 days) post-treatment periods (Fig. 3a). The only strong reduction in estimated mean adjusted daily visitation rate occurred in the heavy feather-clipping group during the first and second post-treatment periods, after which they returned to levels that were similar to unclipped control birds. We found that feeder use differed among periods ($F_{3,14} = 11.30$, $p = 0.010$) but detected no effect of treatment on differences in feeder use among periods ($F_{6,20} = 4.43$, $p = 0.619$). We did find some evidence that mean feeder use differed among treatments in general ($F_{2,14} = 5.92$, $p = 0.052$), with both feather-clipping treatments showing a similar reduction in mean adjusted feeders used compared to the unclipped group, with little difference between the two feather-clipping groups across post-treatment periods (Fig. 3b). Finally, the best supported models for the hourly visitation rate across the day included an effect for time-since-sunrise as well as treatment (Table 1, Fig. 4). Models that included effects of feather-clipping treatments alone were not well-supported across periods and were approximately equivalent in support to a null models (periods 2–4) or were less parsimonious (period 1). Birds in the control group had, on average, more visits throughout all post-sunrise periods, followed by birds in the light feather-clipping treatment and then birds in the heavy-feather clipping treatment. Daily visitation rates increased slightly toward mid-day, and this pattern was similar among birds in all treatments (Fig. 4).

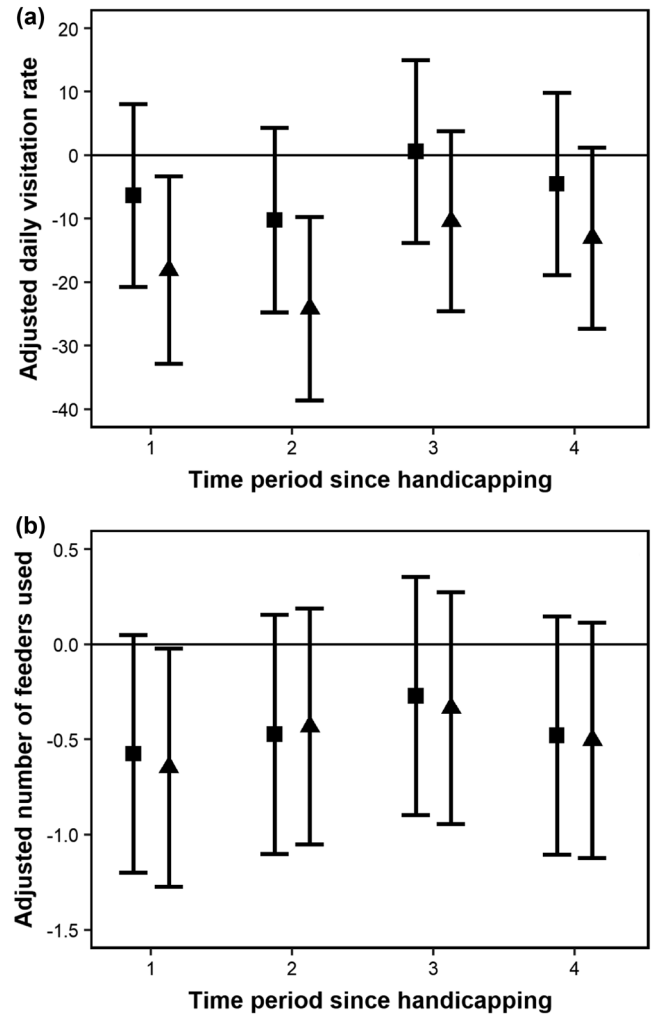


Figure 3. (a) Difference in mean adjusted daily feeder visitation rate from unclipped controls for chickadees in the light feather-clipping treatment (filled squares) and in the heavy feather-clipping treatment (filled triangles) and (b) difference in mean adjusted number of feeders for chickadees in the light feather-clipping treatment (filled squares) and in the heavy feather-clipping treatment (filled triangles) as a function of time period since treatment implementation. Period 1 = 1–5 days post-treatment, period 2 = 6–10 days post-treatment, period 3 = 11–20 days post-treatment and period 4 = 21–30 days post-treatment. Error bars represent 95% Tukey's HSD adjusted confidence intervals correcting for two comparisons at each time period within each panel.

Discussion

Our study found no evidence that experimentally handicapped chickadees increased their rates of visitation to supplemental bird feeders. Instead, removal of primary flight feathers led to a short-term decrease in feeder use by chickadees, with individuals in both feather-clipping treatments using feeders at levels that were similar to unclipped control birds within two weeks. Taken together, these results led us to reject the hypothesis that individuals experiencing elevated flight costs due to feather clipping increased their reliance on supplemental food. However,

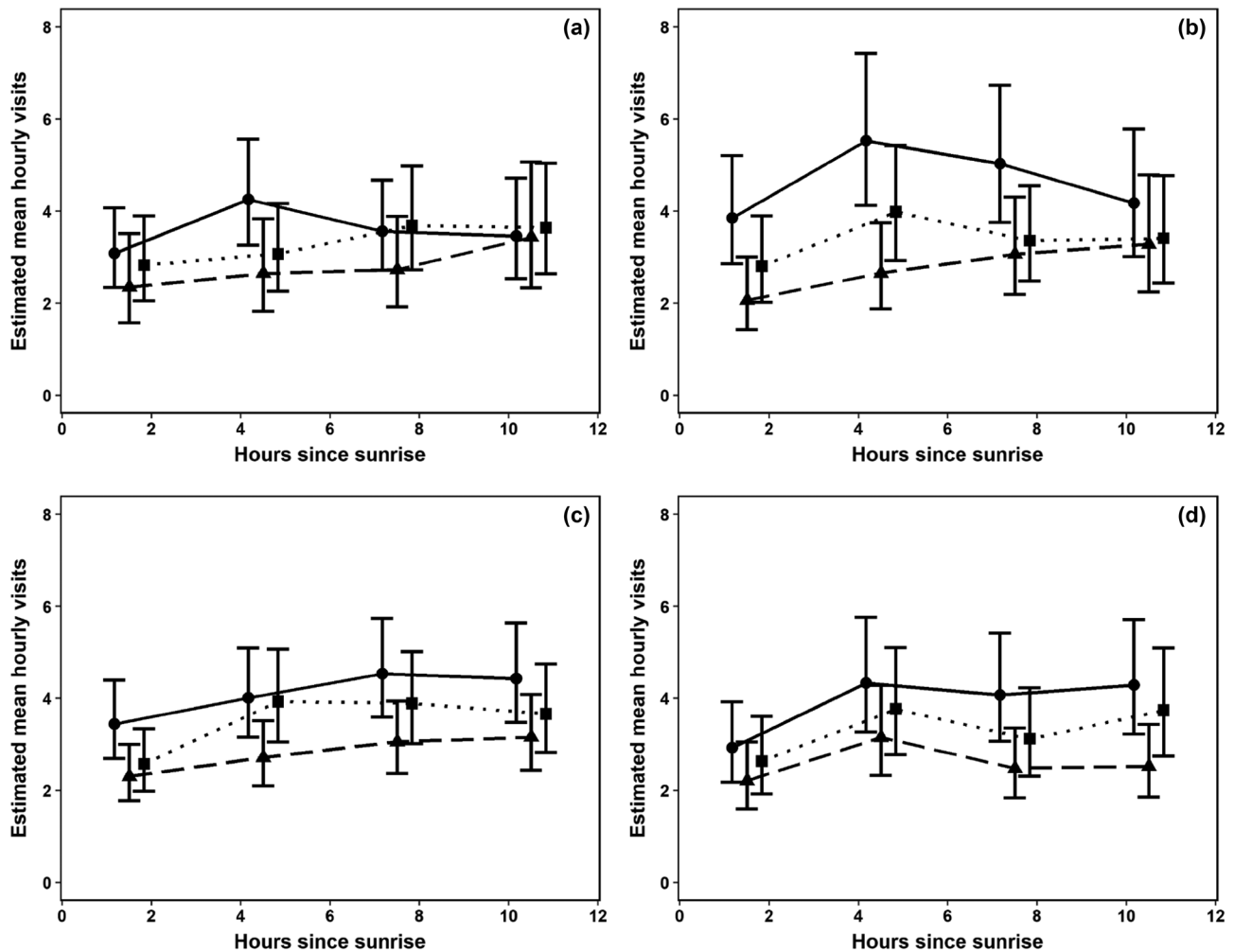


Figure 4. Plot of mean adjusted hourly feeder visitation rates for chickadees in all three treatments during (a) 1–5 days post-treatment, (b) 6–10 days post-treatment, (c) 11–20 days post-treatment and (d) 21–30 days post-treatment. Unclipped control treatment = filled circles and solid lines, light feather-clipping treatment = filled squares and dotted lines, heavy feather-clipping treatment = filled triangles and dashed lines.

we also found no support for the hypothesis that birds avoided RFID-equipped feeders, as all but one of the feather-clipped chickadees returned to feeders after being treated, and because feeder use by feather-clipped birds increased after a brief recovery period. This finding was especially unexpected because feather removal alters wing loading and increases the energetic cost of flight (Pennycuik 1989, Swaddle and Witter 1997, Lind and Jakobsson 2001, Carrascal and Polo 2006), particularly at the high levels that were used in our study (i.e. 22–44 % of primary feathers), and feather-clipped birds should experience elevated energetic demands to retain the same activity levels prior to treatment. Previous work has shown that feather-clipped birds can undergo adaptive physiological changes whereby individuals decrease body mass (Swaddle and Witter 1997, Lind and Jakobsson 2001, Carrascal and Polo 2006) or, in some cases, increase body mass due to size enhancement of pectoral flight muscles (Petit and Vezina 2014). However, such physiological changes are expected to increase energetic expenditure during movement and increase the risk of starvation,

particularly for small birds like the chickadee during winter (Witter and Cuthill 1993, McNamara et al. 1994, Petit and Vezina 2014). Thus, it is puzzling why feather-clipped chickadees in our study did not increase their use of supplemental food, especially if they did increase mass in response to response to feather-clipping.

One explanation for the change in feeder use after handicapping is that feather-clipped birds may have avoided feeders during a period when they acclimated to changes in their flight ability caused by experimental feather removal. In winter, small birds like the chickadee have to balance the risk of predation against the risk of starvation (Lima 1986, McNamara et al. 1994, Brodin 2007), and experimental handicapping leads to a reduction in flight performance (Kullberg et al. 2002b, Senar et al. 2002). Thus, feather-clipped chickadees may have been subject to increased predation risk at feeders and therefore only returned to feeders when their flight ability was adjusted sufficiently to the changes they experienced due to handicapping treatments. That feather-clipped chickadees

reduced their use of feeders relative to control birds suggests that other foods were sufficiently available to feather-clipped birds to compensate for increased flight costs and the reduction in feeder use. Such foods would likely have been natural foods in the environment, cached sunflower seeds from previous feeder visits or both. Seeds, berries and small invertebrates are used by wintering chickadees (Foote et al. 2020) and would be expected to have been available to birds in our study. As noted above, chickadees exhibit food-caching behavior, including sunflower seeds taken from bird feeders (Lima 1985, Barnea and Nottebohm 1995). Although this behavior reaches its peak in autumn (Sherry 1989, Brodin 2005, Hoshooey et al. 2007), there is some evidence of food-caching in spring by close relatives to the chickadee (Pravosudov 2006). Moreover, chickadees can recover cached food items after delays of least four weeks (Hitchcock and Sherry 1990), so it is plausible that birds switched away from using bird feeders and to retrieving caches to offset energetic demands that arose from experimental treatments (Pravosudov 2006). Regardless of the specific mechanism(s) responsible, it is clear that chickadees in our study did not increase their visitation rates as predicted, and that high levels of feather removal had only a transient influence on the use of supplemental feeders by handicapped individuals.

In contrast to daily feeder use patterns, the number of bird feeders used by feather-clipped chickadees showed some decrease relative to unclipped control birds, although the confidence intervals around parameter estimates were large. Previous work has found that birds experiencing feather loss naturally via molt, as well as experimentally feather-clipped individuals, reduce activities that are energetically costly and spend more time in protected areas (Swaddle and Witter 1997, Carrascal and Polo 2006). Thus, the reduction in the number of feeders visited might have been an energy-saving mechanism enacted by feather-clipped individuals. We also found no differences in the time of day that individuals visited feeders in the three treatment groups, which we predicted would be greater for feather-clipped birds. One explanation for this pattern is that feather-clipped birds did indeed have lower energetic reserves in the morning, but they opted to make use of natural food sources and/or cached food items instead of visiting supplemental feeders for sunflower seeds. We were unable to quantify foraging on natural foods or retrieval of food caches in our study, but it is clear that general nutritional requirements are such that chickadees must obtain food from sources beyond the sunflower seeds provided by our bird feeders. An additional, non-mutually exclusive explanation for the pattern we found is that the Mediterranean climate in which we conducted this work experienced overnight temperatures that were unlikely to substantially increase the energetic needs of feather-clipped birds (Lajoie et al. 2019). Thus, additional experiments that use feather-clipping treatments and are conducted in colder climates will be useful to understand the extent to which local environmental conditions interact with experimental handicapping to influence the use of supplemental feeders.

The response variables we measured – the number of feeder visits, the number of feeders used and the timing of feeder visits – varied little between unclipped controls and feather-clipped birds and thus indicate that supplemental bird feeders did not increase in importance when chickadees experienced increased flight costs. That chickadees in our study did not appear reliant on supplemental feeders is concordant with results from the only other study to experimentally test feeder reliance (Brittingham and Temple 1992). Brittingham and Temple (1992) studied color-marked chickadees in two areas, one being a site that had provided supplemental food during winter for 25 years, with the other serving as a control location where no food was offered. Bird feeders were then removed from the feeding site and subsequent apparent survival of chickadees was recorded using a mark-resighting approach (Brittingham and Temple 1992). The authors found that monthly survival rates were similar between the two areas, and chickadees that had used bird feeders in previous winters were equally successful at surviving as those that were not detected using bird feeders (Brittingham and Temple 1992). Although our study and that undertaken by Brittingham and Temple (1992) are fundamentally different in their approach, both provide evidence that chickadees using supplemental feeders in winter do not become reliant on such feeders for their survival, even during energetically demanding periods of low temperatures (Brittingham and Temple 1992) or after experimentally elevated flight costs (this study). As these are the only studies available that have used manipulative experiments to evaluate whether birds are reliant on supplemental feeding, additional work on this topic is needed to understand if these results apply to other bird species and in other ecological settings. In particular, new studies that manipulate energetic demand and are conducted in non-caching songbirds at high latitudes, where cold weather and limited daylight for foraging are typical, will be particularly valuable. Nonetheless, the findings from this study provide critical information that should inform the debate regarding policy guidelines for intentional feeding of wildlife (Reynolds et al. 2017, Baverstock et al. 2019). Going beyond our study, it is clear that intentional feeding can induce a diverse set of biologically relevant changes in bird populations, with some effects only recently uncovered (Bosse et al. 2017, Stostad et al. 2019). Therefore, additional research is needed for a comprehensive understanding of how recreational feeding influences wild, free-ranging bird populations in areas where supplemental feeding is regularly practiced.

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Author contributions

Janel Lajoie: Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Investigation (supporting); Methodology (equal); Writing – original draft (lead); Writing – review and editing (supporting). **Lisa Ganio:** Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Project administration (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Jim Rivers:** Conceptualization (lead); Funding acquisition (lead); Investigation (lead); Project administration (lead); Supervision (equal); Writing – review and editing (equal).

Data availability statement

All data will be published online in Dryad: <<https://doi.org/10.5061/dryad.hdr7sqvj9>> (Lajoie et al. 2021) or similar data repository upon manuscript acceptance.

References

- Adelman, J. S., Moyers, S. C., Farine, D. R. and Hawley, D. M. 2015. Feeder use predicts both acquisition and transmission of a contagious pathogen in a North American songbird. – *Proc. R. Soc. B* 282: 20151429.
- Baicich, P. J., Barker, M. A. and Henderson, C. L. 2015. Feeding wild birds in America: culture, commerce and conservation. – Texas A&M Univ. Press.
- Barnea, A. and Nottebohm, F. 1995. Patterns of food storing by black-capped chickadees suggest a mnemonic hypothesis. – *Anim. Behav.* 49: 1161–1176.
- Baverstock, S., Weston, M. A. and Miller, K. K. 2019. A global paucity of wild bird feeding policy. – *Sci. Total Environ.* 653: 105–111.
- Becker, D. J., Streicker, D. G. and Altizer, S. 2015. Linking anthropogenic resources to wildlife–pathogen dynamics: a review and meta-analysis. – *Ecol. Lett.* 18: 483–495.
- Bonter, D. N. and Bridge, E. S. 2011. Applications of radio frequency identification (RFID) in ornithological research: a review. – *J. Field Ornithol.* 82: 1–10.
- Bonter, D. N., Zuckerberg, B., Sedgwick, C. W. and Hochachka, W. M. 2013. Daily foraging patterns in free living birds: exploring the predation–starvation tradeoff. – *Proc. R. Soc. B* 280: 20123087.
- Bosse, M., Spurgin, L. G., Laine, V. N., Cole, E. F., Firth, J. A., Gienapp, P., Gosler, A. G., McMahon, K., Poissant, J., Verhagen, I., Groenen, M. A. M., van Oers, K., Sheldon, B. C., Visser, M. E. and Slate, J. 2017. Recent natural selection causes adaptive evolution of an avian polygenic trait. – *Science* 358: 365–368.
- Bridge, E. and Bonter, D. N. 2011. A low-cost radio frequency identification device for ornithological research. – *J. Field Ornithol.* 82: 52–59.
- Brittingham, M. C. and Temple, S. A. 1988. Impacts of supplemental feeding on survival rates of black-capped chickadees. – *Ecology* 69: 581–589.
- Brittingham, M. C. and Temple, S. A. 1992. Does winter bird feeding promote dependency? – *J. Field Ornithol.* 63: 190–194.
- Brodin, A. 2005. Hippocampal volume does not correlate with food-hoarding rates in the black-capped chickadee *Poecile atricapillus* and willow tit *Parus montanus*. – *Auk* 122: 819–828.
- Brodin, A. 2007. Theoretical models of adaptive energy management in small wintering birds. – *Phil. Trans. R. Soc. B* 362: 1857–1871.
- Broggi, J., Hohtola, E. and Koivula, K. 2021. Winter feeding influences the cost of living in boreal passerines. – *Ibis* 163: 260–267.
- Burnham, K. P. and Anderson, D. R. 2004. Multimodel inference: understanding AIC and BIC in model selection. – *Sociol. Methods Res.* 33: 261–304.
- Carrascal, L. M. and Polo, V. 2006. Effects of wing area reduction on winter body mass and foraging behaviour in coal tits: field and aviary experiments. – *Anim. Behav.* 72: 663–672.
- Cox, D. T. C. and Gaston, K. J. 2018. Human–nature interaction and the consequences and drivers of provisioning wildlife. – *Phil. Trans. R. Soc. B* 373: 20170092.
- Danner, R. M., Greenberg, R. S., Danner, J. E., Kirkpatrick, L. T. and Walters, J. R. 2013. Experimental support for food limitation of a short-distance migratory bird wintering in the temperate zone. – *Ecology* 94: 2803–2816.
- Davies, Z. G., Fuller, R. A., Dallimer, M., Loram, A. and Gaston, K. J. 2012. Household factors influencing participation in bird feeding activity: a national scale analysis. – *PLoS One* 7: e39692.
- Desrochers, A. and Turcotte, Y. 2008. Forest fragmentation and body condition in wintering black-capped chickadees. – *Can. J. Zool.* 86: 572–581.
- Dunn, E. H. and Tessaglia, D. L. 1994. Predation of birds at feeders in winter. – *J. Field Ornithol.* 65: 8–16.
- Ficken, M. S., Weise, C. M. and Popp, J. W. 1990. Dominance rank and resource access in winter flocks of black-capped chickadees. – *Wilson Bull.* 102: 623–633.
- Foote, J. R., Mennill, D. J., Ratcliffe, L. M. and Smith, S. M. 2020. Black-capped chickadee *Poecile atricapillus*, ver. 1.0. – In: Poole, A. F. (ed.), *Birds of the world*. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Galbraith, J. A., Beggs, J. R., Jones, D. N. and Stanley, M. C. 2015. Supplementary feeding restructures urban bird communities. – *Proc. Natl Acad. Sci. USA* 112: E2648–E2657.
- Hitchcock, C. L. and Sherry, D. F. 1990. Long-term memory for cache sites in the black-capped chickadee. – *Anim. Behav.* 40: 701–712.
- Hoshooley, J. S., Phillimore, L. S., Sherry, D. F. and MacDougall-Shackleton, S. A. 2007. Annual cycle of the black-capped chickadee: seasonality of food-storing and the hippocampus. – *Brain Behav. Evol.* 69: 161–168.
- Ishigame, G. and Baxter, G. S. 2007. Practice and attitudes of suburban and rural dwellers to feeding wild birds in southeast Queensland, Australia. – *Ornithol. Sci.* 6: 11–19.
- Jones, D. 2018. *The birds at my table: why we feed wild birds and why it matters*. – Cornell Univ. Press.
- Jones, D. N. and Reynolds, S. J. 2008. Feeding birds in our towns and cities: a global research opportunity. – *J. Avian Biol.* 39: 265–271.
- Karasov, W. H., Brittingham, M. C. and Temple, S. A. 1992. Daily energy and expenditure by black-capped chickadees *Parus atricapillus* in winter. – *Auk* 109: 393–395.
- Kessel, B. 1976. Winter activity patterns of black-capped chickadees in interior Alaska. – *Wilson Bull.* 88: 36–61.
- Kullberg, C. and Lafrenz, M. 2007. Escape take-off strategies in birds: the significance of protective cover. – *Behav. Ecol. Sociobiol.* 61: 1555–1560.
- Kullberg, C., Jakobsson, S. and Fransson, T. 1998. Predator-induced take-off strategy in great tits *Parus major*. – *Proc. R. Soc. B* 265: 1659–1664.
- Kullberg, C., Metcalfe, N. B. and Houston, D. C. 2002a. Impaired flight ability during incubation in the pied flycatcher. – *J. Avian Biol.* 33: 179–183.

- Kullberg, C., Houston, D. C. and Metcalfe, N. B. 2002b. Impaired flight ability – a cost of reproduction in female blue tits. – *Behav. Ecol.* 13: 575–579.
- Lajoie, J. L. 2018. Supplemental feeder use by free-living black-capped chickadees *Poecile atricapillus* in a Mediterranean climate. – MSc thesis, Oregon State Univ.
- Lajoie, J. L., Ganio, L. M. and Rivers, J. W. 2019. Individual variation and seasonality drive bird feeder use during winter in a Mediterranean climate. – *Ecol. Evol.* 9: 2535–2549.
- Lajoie, J. L., Ganio, L. M. and Rivers, J. W. 2021. Data from: Experimentally induced flight costs do not lead to increased reliance on supplemental food in winter by a small songbird. – Dryad, <<https://doi.org/10.5061/dryad.hdr7sqvj9>>.
- Lima, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. – *Oecologia* 66: 60–67.
- Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. – *Ecology* 67: 377–385.
- Lind, J. and Jakobsson, S. 2001. Body building and concurrent mass loss: flight adaptations in tree sparrows. – *Proc. R. Soc. B* 268: 1915–1919.
- Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., Sadat, N., Ludecke, D., Lenth, R., O'Brien, J. and Brooks, M. 2020. Generalized linear mixed models using template model builder. – <<https://github.com/glmmTMB/glmmTMB>>.
- Malpass, J. S., Rodewald, A. D. and Matthews, S. N. 2017. Species-dependent effects of bird feeders on nest predators and nest survival of urban American robins and northern cardinals. – *Condor* 119: 1–16.
- McNamara, J. M., Houston, A. I. and Lima, S. L. 1994. Foraging routines of small birds in winter: a theoretical investigation. – *J. Avian Biol.* 25: 287–302.
- National Oceanic and Atmospheric Administration (NOAA) 2021. NOAA Solar Calculator. – <<https://gml.noaa.gov/grad/solcalc/>>.
- Pennycuik, C. J. 1989. Bird flight performance: a practical calculation manual. – Oxford Univ. Press.
- Petit, M. and Vezina, F. 2014. Phenotype manipulations confirm the role of pectoral muscles and hematocrit in avian maximal thermogenic capacity. – *J. Exp. Biol.* 217: 824–830.
- Pinheiro, J., Bates, D., Debroy, S., Sarkar, D. and R Core Team. 2021. Linear and nonlinear mixed effects models. – <<https://CRAN.R-project.org/package=nlme>>.
- Plummer, K. E., Bearhop, S., Leech, D. I., Chamberlain, D. I. and Blount, J. D. 2013a. Winter food provisioning reduces future breeding performance in a wild bird. – *Sci. Rep.* 3: article 2002.
- Plummer, K. E., Bearhop, S., Leech, D. I., Chamberlain, D. E. and Blount, J. D. 2013b. Fat provisioning in winter impairs egg production during the following spring: a landscape-scale study of blue tits. – *J. Anim. Ecol.* 82: 673–682.
- Plummer, K. E., Siriwardena, G. M., Conway, G. J., Risely, K. and Toms, M. P. 2015. Is supplementary feeding in gardens a driver of evolutionary change in migratory bird species? – *Global Change Biol.* 21: 4353–4363.
- Pravosudov, V. V. 2006. On seasonality in food-storing behavior in parids: do we know the whole story? – *Anim. Behav.* 71: 1455–1460.
- Pravosudov, V. V. 2007. The relationship between environment, corticosterone, food caching, spatial memory and the hippocampus in chickadees. – In: Otter, K. A. (ed.), *Ecology and behavior of chickadees and titmice: an integrated approach*. Oxford Univ. Press, pp. 25–41.
- Reynolds, S. J., Galbraith, J. A., Smith, J. A. and Jones, D. N. 2017. Garden bird feeding: insights and prospects from a north–south comparison of this global urban phenomenon. – *Front. Ecol. Evol.* 5: article 24.
- Rickett, J., Dey, C. J., Stothart, J., O'Connor, C. M., Quinn, J. S. and Ji, W. 2013. The influence of supplemental feeding on survival, dispersal and competition in translocated brown teal, or pateke *Anas chlorotis*. – *Emu* 113: 62–68.
- Rivers, J. W., Newberry, G. N., Schwarz, C. J. and Ardia, D. R. 2017. Success despite the stress: violet-green swallows increase glucocorticoids and maintain reproductive output following experimental increases in flight costs. – *Funct. Ecol.* 31: 235–244.
- Robb, G. N., McDonald, R. A., Chamberlain, D. E., Reynolds, S. J., Harrison, T. J. E. and Bearhop, S. 2008a. Winter feeding of birds increases productivity in the subsequent breeding season. – *Biol. Lett.* 4: 220–223.
- Robb, G. N., McDonald, R. A., Chamberlain, D. E. and Bearhop, S. 2008b. Food for thought: supplementary feeding as a driver of ecological change in avian populations. – *Front. Ecol. Environ.* 6: 476–484.
- Senar, J. C., Domenech, J. and Urbie, F. 2002. Great tits *Parus major* reduce body mass in response to wing area reduction: a field experiment. – *Behav. Ecol.* 13: 725–727.
- Sherry, D. F. 1989. Food storing in the Paridae. – *Wilson Bull.* 101: 289–304.
- Smith, S. M. 1991. The black-capped chickadee: behavioral ecology and natural history. – Cornell Univ. Press.
- Stostad, H. N., Rowe, M., Johnsen, A., Tomasek, O., Albrecht, T. and Lifeld, J. T. 2019. Sperm head abnormalities are associated with excessive omega-6 fatty acids in two finch species feeding on sunflower seeds. – *J. Avian Biol.* 50: e02056.
- Swaddle, J. P. and Witter, M. S. 1997. The effects of molt on the flight performance, body mass and behavior of European starlings *Sturnus vulgaris*: an experimental approach. – *Can. J. Zool.* 75: 1135–1146.
- Swaddle, J. P., Williams, E. V. and Rayner, J. M. V. 1999. The effect of simulated flight feather molt on escape take-off performance in starlings. – *J. Avian Biol.* 30: 351–358.
- Turner, S., Demers, E., Norris, K. and Wheeler, D. 2020. Application of radio frequency identification technology to study nesting behaviour of tree swallows. – *North Am. Bird Bander* 45: 81–95.
- U.S. Fish and Wildlife Service (USFWS) 2011. The 2011 national survey of fishing, hunting and wildlife-associated recreation. – U.S. Fish and Wildlife Service, Virginia, USA.
- Wasserstein, R. L. and Lazar, N. A. 2016. The A.S.A.'s statement on p-values: context, process and purpose. – *Am. Stat.* 70: 129–133.
- Wilcoxon, T. E., Horn, D. J., Hogan, B. M., Hubble, C. N., Huber, S. J., Flamm, J., Knott, M., Lundstrom, L., Salik, F., Wassenhove, S. J. and Wrobel, E. R. 2015. Effects of bird-feeding activities on the health of wild birds conservation. – *Conserv. Physiol.* 3: cov058.
- Witter, M. S. and Cuthill, I. C. C. 1993. The ecological costs of avian fat storage. – *Phil. Trans. R. Soc. B* 340: 73–92.