

Experimental evidence and 43 years of monitoring data show that food limits reproduction in a food-caching passerine

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Abstract. Several species of birds and mammals overcome periods of scarcity by caching food, but for the vast majority of species, it is virtually unknown whether they are food limited during these periods. The Gray Jay (*Perisoreus canadensis*) is a boreal-resident, food-caching passerine that breeds in late winter when fresh food is scarce. Using a two-year experiment and 43 years of monitoring data, we examined the food limitation hypothesis in a population of Gray Jays in Algonquin Park, Ontario, Canada, that has declined by over 50% in the last three decades. Breeding pairs that were experimentally food supplemented during the pre-breeding period laid eggs earlier in the season and had larger brood sizes than non-supplemented controls. From the long-term data, we found strong evidence that pairs that were regularly supplemented by the public (park visitors) tended to lay eggs earlier and have larger clutches and brood sizes compared to pairs that were not supplemented. Nestling body condition (mass controlled for body size) was not influenced by either experimental or public food supplementation. Our results support the hypothesis that Gray Jays are food limited during their late-winter breeding period and suggest that warmer fall temperatures, which have been hypothesized to lead to cache spoilage, may have a significant impact on reproductive success in this declining population. Moreover, our results contribute to understanding how public feeding can influence the fitness of wild animals.

Key words: Algonquin Park, Ontario, Canada; caching; food limitation; food supplementation; Gray Jay; long-term data; *Perisoreus canadensis*; population decline; public feeding; reproduction.

INTRODUCTION

It is well established in a wide range of animals that reproduction is energetically costly (Gittleman and Thompson 1988, Olsson et al. 1997, Watson et al. 1998, Hendry and Berg 1999, Fernández et al. 2000, Brand and Bowman 2012). High energy demands are associated with multiple stages of the reproductive cycle, for example the construction of nests (Gauthier and Thomas 1993, Nilsson and Råberg 2001, Mikheyev and Tschinkel 2004), the production of eggs in oviparous species (Fitzpatrick 1973, Vance 1973, Tallamy and Denno 1982, Vézina and Williams 2005), brooding and incubating (Fitzpatrick 1973, Tallamy and Denno 1982, Fernández et al. 2000, Hanssen et al. 2003, Lardies et al. 2004), gestation and lactation in mammals (Gittleman and Thompson 1988, Clutton-Brock et al. 1989), and care of young until independence in altricial species (Gittleman and Thompson 1988, Daan et al. 1990, Steinhart et al. 2005). Because of the elevated energy demand associated with reproduction, evidence suggests that food availability can have important consequences for reproductive performance (Martin 1987, Boutin 1990). Observational studies have shown that reproduc-

tive performance in multiple taxa increases in years or territories associated with high natural food availability (Thresher 1985, Morrison and Bolger 2002, Boutin et al. 2006). Experimentally increasing food availability in animal populations has been shown to advance the timing of breeding (Lenski 1984, Reynolds et al. 2003a, Du 2006, Kerr et al. 2007), increase the number of offspring produced (Wise 1979, Högstedt 1981, Vanni 1987, Guyer 1988, Reynolds et al. 2003a), improve the nutritional condition of offspring, as measured by offspring body size and mass (Arcese and Smith 1988, Simons and Martin 1990, Samhuri 2009), lead to more breeding attempts (Arcese and Smith 1988, Taylor et al. 2005, Du 2006), and result in a larger number of young produced to independence (Dhindsa and Boag 1990, Ridgway and Shuter 1994, Kerr et al. 2007). Together, these observational and experimental studies provide evidence that periods of food scarcity during the breeding season may cause declines in reproductive success.

Caching is a strategy to overcome periods of food scarcity and is a behavior that occurs in a variety of birds and mammals (Vander Wall 1990), primarily, but not exclusively, at northern latitudes (Smith and Reichman 1984). Some caching species rely on stored food even during the reproductive period: the Piñon Jay *Gymnorhinus cyanocephalus* (Ligon 1978), the Boreal Owl *Aegolius funereus* (Korpimäki 1987), the Burrowing

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Owl *Speotyto cunicularia* (Wellicome 2005), and the wolverine *Gulo gulo* (Inman et al. 2012). Although evidence generally supports the food limitation hypothesis for species that consume fresh food during the breeding season, few studies have examined food limitation in animals that rely on stored food during reproduction (Ligon 1978, Korpimäki 1987, Wellicome 2005). On the one hand, it seems reasonable to hypothesize that caching is an adaptation that overcomes food limitation, given that caching species can be extremely effective at storing large amounts of resources that are preserved for long periods (Vander Wall 1990). For example, the Boreal Owl relies on cached food to feed nestlings during temporary shortages of fresh food (Korpimäki 1987). Alternatively, there could be selective pressures, such as long developmental time of young (Inman et al. 2012), that force food-caching species to breed outside the time period that would otherwise be optimal based on food abundance. If so, these species may be food limited in the breeding season and this could be exacerbated, at times, by cache robbing or food spoilage (Vander Wall 1990, Inman et al. 2012).

We tested whether or not reproduction was limited by food availability in the Gray Jay (*Perisoreus canadensis*; see Plate 1), a nonmigratory, food-caching passerine of North America's boreal and subalpine forests (Strickland and Ouellet 2011). Most food-caching birds store seeds or nuts that are resistant to spoilage (Vander Wall 1990), but Gray Jays store only perishable food items, such as arthropods, berries, mushrooms, and meat from carcasses (Strickland and Ouellet 2011). Gray Jays rely on cached food to survive the winter and for all or part of their breeding cycle, which commences as early as mid-February during subzero temperatures (Strickland and Ouellet 2011). In Algonquin Park, Ontario, Canada, Gray Jays have declined by over 50% over the past three decades (Strickland et al. 2011) and one hypothesis to explain these declines is that warmer fall temperatures are spoiling cached food, which then carries over to influence reproductive success (Waite and Strickland 2006). A key assumption of this hypothesis is that reproductive performance in Gray Jays is limited by food abundance.

There is some evidence for food limitation during the breeding season in Gray Jays. Waite and Strickland (2006) found that the reproductive success of Gray Jays in Algonquin Park, Ontario, was predicted, in part, by whether breeding pairs occupied territories that were supplemented by feeders or the public (park visitors). However, they were not able to control for the quality or quantity of food fed to pairs and the analysis did not account for female age or the fact that females bred over multiple years, making them nonindependent samples (Waite and Strickland 2006). Here, we conducted both a food supplementation experiment over two years and an analysis of 43 years of monitoring data using mixed-effects models to account for individual variation in both reproductive output and age. Following the food

limitation hypothesis, we predicted that breeding pairs provided with supplemental food would have higher reproductive success, as measured by earlier lay date, higher clutch size, larger brood size, and higher nestling body condition, compared to non-supplemented control pairs.

METHODS

Study area and species

We conducted our study in Algonquin Provincial Park, Ontario, Canada (45° N, 78° W; >7.6 × 10⁵ ha), where the reproductive performance and survival of a Gray Jay population has been monitored since the 1960s (Rutter 1969, Strickland 1991, Strickland and Waite 2001, Norris et al. 2013). The study site runs mainly along the highway 60 corridor, which transects the park, and currently contains ~30 occupied territories of ~130 ha each. The population is sedentary and food storage behavior is conspicuous from late August through fall and opportunistic in winter. Individual food items are hidden under tree bark and arboreal lichens (Strickland et al. 2011) with the aid of copious sticky saliva (Dow 1965). Algonquin Gray Jays typically begin nesting in March, with the earliest lay date recorded in late February (Strickland and Ouellet 2011). Pairs produce a single brood per season, although replacement nests can be built if the first nest fails during the incubation period and early (before 10 April) in the breeding season (Strickland and Ouellet 2011). All jays within the population are banded (Banding Permit No. 10416) with a unique combination of three color leg bands in addition to a standard Canadian Wildlife Service aluminum leg band as nestlings (age range 8–14 d) or when discovered as newly dispersed immigrants into the study area. Ages of the latter are estimated as juvenile (first-year) or adult (second-year or older) bird, using retrix shape (Strickland and Ouellet 2011).

Experimental food supplementation

We conducted a food supplementation experiment during the pre-breeding period (31 January–26 February) over two years (2013, 2014). We chose to supplement Gray Jays with high-protein cat food, given evidence that protein influences reproductive success in birds (Meijer and Drent 1999, Reynolds et al. 2003a, b). In 2013, we blended IAMS Proactive Health Kitten dry kibble (IAMS, Leipsic, Ohio, USA; 37% DM protein, 23% DM fat) with a 1:1 ratio of water (by mass) and then partially dried it in a conventional oven or on a stovetop. The food was blended with water so that we could add powdered glycine containing the heavy isotope form of nitrogen (¹⁵N) as part of a separate stable nitrogen isotope experiment. The glycine did not influence the nutritional content of the food. In 2014, we switched to canned IAMS Adult Premium Pâté with Gourmet Chicken (IAMS, Pennsauken, New Jersey, USA) because we determined that the consistency of this food was better suited for the addition of the powdered

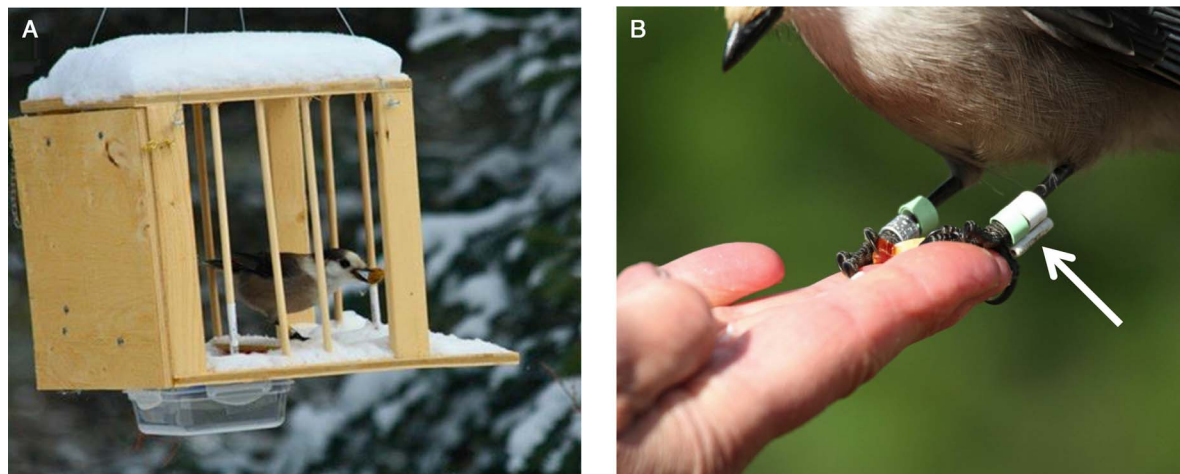


FIG. 1. Feeder design for the food supplementation experiment. (A) A Gray Jay (*Perisoreus canadensis*) about to exit the feeder with supplemented food in its bill (photo credit: Talia Sechley). An antenna across the front of the feeder was connected to a Radio Frequency Identification (RFID) reader housed in a small plastic box under the feeder. (B) The white RFID tag attached to the leg bands on the left leg of a female (indicated by the arrow; photo credit: Gord Belyea). See Appendix A for details of feeder construction.

glycine. This food had a similar amount of protein (45% DM, compared to 37% DM in the kibble), the same amount of fat (23% DM), and contained the same protein source (domestic chicken; *Gallus gallus domesticus*) as the kibble used in 2013. As in 2013, this food was also blended with a small amount of water and then partially dried before it was provided to jays.

All food was packaged into 800-g quantities. After drying, we estimated that the kibble contained 10 435 J/g and the canned food contained 5962 J/g (~1000 g of blended food would dry down to one 800-g package). Although the canned food had fewer joules per serving than the kibble, we attempted to keep protein consistent between seasons rather than ensuring consistent intake of joules, because evidence suggests that protein is more limiting for avian reproduction than are joules (Meijer and Drent 1999, Reynolds et al. 2003a, b). Moreover, even with the reduced joules in the canned food, the average amount of food provided to each territory in 2014 was ~43 986 kJ. This ensured that the total amount supplied for the entire supplementation period exceeded a pair's breeding-season needs, based on an estimated daily energy requirement of 197 kJ in a 90-d breeding season (Strickland and Ouellet 2011), and assuming that all the food in the feeder was consumed by the breeding pair.

We supplemented 20 breeding pairs ($n = 10$ in both 2013 and 2014) and the remaining breeding pairs acted as controls ($n = 13$ in both 2013 and 2014). Supplemented territories were selected to maximize the efficiency of checking feeders in a timely manner each day while being certain that the selected territories spanned a range of public accessibility and that no territory was supplemented in two consecutive years. Supplemental food was provided to females and males

using feeders that were designed to minimize the access of other animal species to the food and allowed us to track the number of times females entered each feeder using Radio Frequency Identification (RFID) tags (unique 2.12×12.0 mm glass tags, #601201; Cyntag, Cynthiana, Kentucky, USA) and RFID readers (Fig. 1; see details of feeder design and operation in Appendix A). We placed the feeders at least 100 m from the boundary of each treatment territory (mean territory size in Algonquin Park is 129 ha; Strickland and Ouellet 2011) to prevent jays in any occupied adjacent territories from accessing the food. Each feeder was checked daily and refilled with 800 g of food if it was more than half empty, as estimated by eye. We estimated feeding rate as the total number of RFID fixes per day divided by two, because we assumed that the tag was recorded when the female was both entering and leaving the feeder. This estimate was used only to confirm that females were indeed accessing the supplemental food on a regular basis and was not used as a predictor in any of our models. For the experimental feeders in which the RFID readers worked for a minimum of 25 d ($n = 4$ for 2013; $n = 5$ for 2014), females, on average, entered on 13 ± 2 d (mean \pm SD; range 4–22 d) of the 27 d supplementation period. For feeders in which we could record reliable (i.e., continuous readings) visitation rates within a day ($n = 9$ feeders), females entered an average of 36 ± 8 times per day (range 2–73).

After supplementation, we tracked the reproductive performance of pairs on both supplemented and control territories. Measured or estimated reproductive variables were: lay date, clutch size, brood size (measured at ~11 d of age), and nestling body condition. Because females rarely leave the nest once they have laid the first egg (Strickland and Ouellet 2011), lay date was



PLATE 1. Gray Jays live on permanent boreal forest territories and nest under seemingly foodless conditions in late winter. This photograph, taken on 3 April 1969 in Parc de la Vérendrye, Québec, Canada, represent a typical scene during the Gray Jay breeding season: an incubating female two days after a snowstorm and one day before the three eggs hatched. Photo credit: D. Strickland.

estimated as the first day that the female was observed sitting on the nest (nests were visited daily leading up to the beginning of laying). Gray Jays keep eggs warm but do not begin incubation until the full clutch is laid (Strickland and Ouellet 2011). Because incubation lasts 18 d (Strickland and Ouellet 2011), we estimated hatching date based on a modal clutch size of three. In 2014, the exact lay date could not be estimated for three females, so these females were observed during the probable “hatch window” for evidence of shell eating or feeding of nestlings and the lay date was back-calculated from the inferred hatch date. Nestlings were banded when ~ 11 d old, the nest being accessed by ladder (if < 9 m high) or by a professional tree-climber (if > 9 m high). However, we were not always able to access the nest on day 11 post-hatch due to weather and other logistical reasons (in 2013, $n = 16$ nests, nestling age range when accessed was 7–12 d; in 2014, $n = 15$ nests, age range when accessed was 8–14 d). Nestlings and unhatched eggs were then counted. In all but three cases where the inside of nests could be directly observed using a mirror pole (2013, $n = 2$; 2014, $n = 1$), we estimated clutch size by adding the number of unhatched eggs to the brood size at the time the nest was accessed to band and measure nestlings. In total, 53 first or replacement nests in which a clutch was initiated were located (2013, $n =$

25; 2014, $n = 28$) in the territories of 30 females (2013, $n = 24$; 2014, $n = 25$; 19 females bred in both years) and 106 nestlings were banded from 38 nests (2013, $n = 56$ nestlings from 20 nests; 2014, $n = 50$ nestlings from 18 nests).

To estimate nestling condition, we first conducted a principal component analysis (PCA; Duntelman 1989, Rising and Somers 1989) from a correlation matrix of 417 tarsus, seventh primary, and bill length measurements taken from 77 known-age nestlings from the long-term data (details about the PCA and loadings on all three axes can be found in Appendix B). The principal component scores from the first axis were a good predictor of age ($R^2 = 0.94$, $b = 2.37$, $P < 0.001$). We then modeled the relationship between mass and PC1 scores for these nestlings and used the residuals from this model to generate an estimate of condition (mass given body size) for unknown-age nestlings (see additional details in Appendix B).

Four supplemented territories were excluded from analysis because the female did not develop a pair bond or permanently occupy a territory ($n = 1$ in 2013) or, based on the data from the RFID readers, the female never accessed the feeder (2013, $n = 2$; 2014, $n = 1$). In six cases, nests failed during the nestling period so we were only able to record lay date (2013, $n = 1$ supplemented

nest; 2014, $n = 1$ supplemented nest, $n = 4$ control nests). For two additional nests, both lay date and clutch size were known but the nest failed before banding (2013, $n = 1$ control nest; 2014, $n = 1$ control nest). One territory was not included as either a treatment or control in both years because the jays occupying this territory received a substantial amount of supplemental food from park visitors. By “substantial,” we mean that the pair was being fed by the public during the majority of our visits to the territory and the territory is also a well-publicized location to feed Gray Jays in the Park.

Long-term data: supplementation by the public

We used data collected from 1970–2012 (excluding 1973–1976 when no data were collected) to examine the reproductive performance of uniquely banded pairs that nested on territories that were regularly supplemented by the public (park visitors) vs. those not supplemented by the public. Gray Jays seek and accept food from humans during the fall and winter when fresh food is not readily available. Because our study site runs partly along the main highway through the park, several monitored territories contained trail heads or other facilities heavily used by park visitors, whereas other territories were located in more remote areas. Because we did not quantify the level of visitation over these years, we conducted a post hoc classification based on personal observation. We classified 39 of 59 territories occupied between 1970 and 2012 as having either a “low” or “high” level of supplementation. We considered territories to have a high level of supplementation ($n = 14$ territories, 65 females, 174 nests) if there was either a permanent feeder, or visitors were commonly observed feeding jays. Territories were deemed to have a low level of supplementation ($n = 26$ territories, 65 females, 220 nests) if they were far (>200 m from territory boundary) from roads or walking trails and rarely, if ever, accessed by the public. We excluded 20 territories because they were not easily classified into one of these two groups (i.e., had irregular visitation rates by the public). One territory was designated as receiving a low level of supplementation until 1992, when the current Visitor Centre was built and the territory was reclassified as receiving a high level of supplementation.

Of the 394 nests in the long-term data, not all of our measures of reproductive success were recorded or estimated for each nest. Lay date was recorded for 389 nests, clutch size was recorded for 325 nests, and brood size was recorded for 375 nests. Of the 375 nests recorded for brood size, 98 of these failed during the nestling period (brood size = 0). We excluded these failed nests from our analysis of the effect of supplementation on brood size because supplementation did not significantly improve the fit of a nest success model based on a likelihood ratio test (see *Statistical methods*). In some cases, not all nestling morphometric data were taken, so we could only estimate nestling condition for 259 nests.

Statistical methods

To understand how food availability influenced reproductive success, we constructed a series of linear mixed-effects models using lme4 (R package v. 3.0-1; Bates et al. 2014) and used model selection (likelihood ratio tests) to evaluate whether supplementation was a significant predictor of reproductive success. The ‘global’ linear mixed-effects model for each response variable (lay date, clutch size, brood size, and nestling condition) included the following independent variables: supplementation level (high or low for the long-term data; treatment or control for the experiment) and female age as fixed effects, and female identity and year as random effects. Female age was included in all models because previous evidence suggests that female reproductive success increases with age (Strickland et al. 2011, Sechley et al. 2013). We included female identity as a random effect because some females bred in multiple years, and year was included as a random effect because of differences in environmental conditions between years that may have influenced food availability and reproductive success. We constructed a similar mixed-effects model to test whether nest failure was influenced by supplementation in the long-term data, because some studies have shown an effect of supplementation on adult nest attendance or predation rates (Ewald and Rohwer 1982, Ward and Kennedy 1996, Dewey and Kennedy 2001). The global model was a generalized linear mixed-effects model with a binomial distribution, the same predictor variables (female age and supplementation level as fixed effects; year and female identity as random effects), and with nest failure (yes/no) as the response variable. We then removed supplementation level from each global model to generate a second set of models for each response variable. To assess whether supplementation level significantly improved the model fit, we compared the reduced model to the global model using the likelihood ratio test statistic (Vuong 1989) for each response variable, using an alpha level of 0.05. Effect sizes are presented with standard error. All statistical tests and calculations were performed using R v. 3.0-1 (R Development Core Team 2013).

RESULTS

Supplementation by the public did not significantly improve model fit for the nest failure model in the long-term data ($\chi^2 = 0.5$, $df = 1$, $P = 0.47$). Therefore, we did not include failed nests in our brood size models for either the experiment or the long-term data, and instead tested how supplementation influenced brood size for nests that did not fail before banding day.

Experimental supplementation significantly improved the model fit to explain lay date ($\chi^2 = 20.9$, $df = 1$, $P < 0.001$; Fig. 2A), and the model predicted that supplemented females would lay eggs 8.9 ± 1.7 d (mean \pm SE) earlier than controls. Experimental supplementation did not significantly improve the model fit to explain clutch size ($\chi^2 = 2.8$, $df = 1$, $P = 0.10$; Fig. 2B), but it did

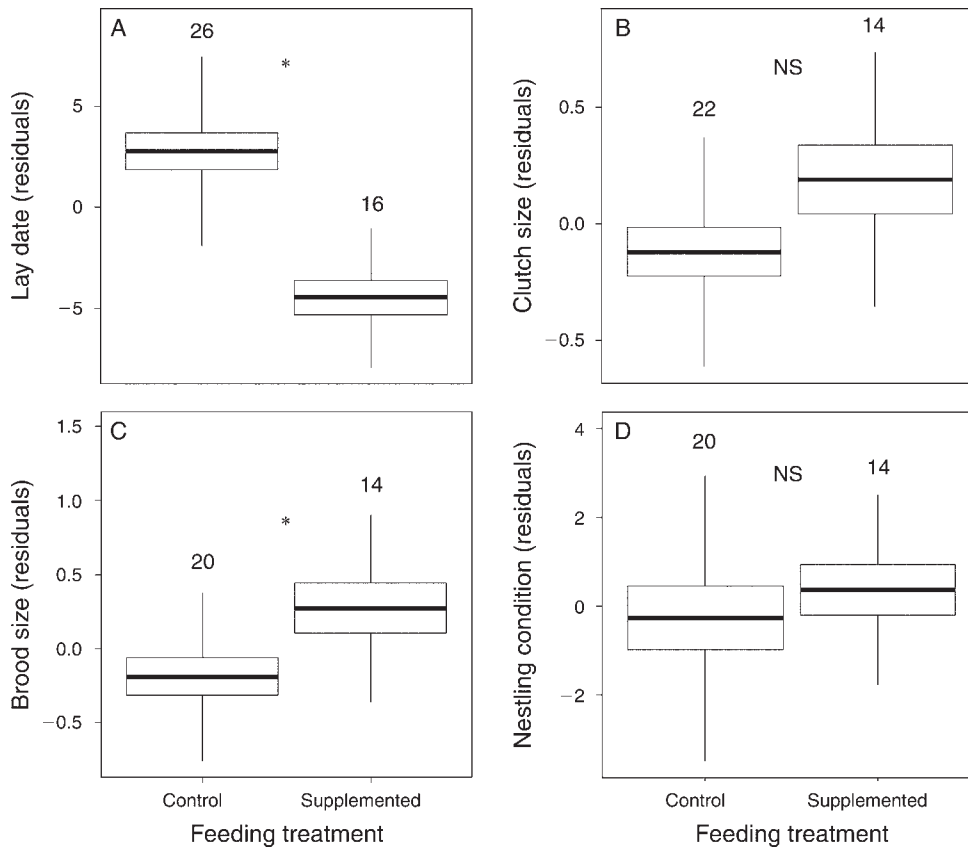


FIG. 2. Experimental effect of food supplementation on model residuals for linear mixed-effects models that modeled the effects of female age, female identity (random effect), and year (random effect) on (A) lay date, (B) clutch size, (C) brood size, and (D) nestling condition for Gray Jays in Algonquin Park, Ontario, Canada. The thick line within each box represents the mean, the lower and upper limits of the box represent the standard error of the mean, and the vertical whiskers are the standard deviation. Sample sizes are given above each plot. An asterisk indicates statistical significance ($P < 0.05$); NS indicates nonsignificance ($P \geq 0.05$).

significantly improve the model fit for brood size ($\chi^2 = 5.3$, $df = 1$, $P = 0.02$; Fig. 2C). Experimentally supplemented pairs were predicted to have 0.7 ± 0.3 more nestlings in their broods than controls. Supplementation did not significantly improve the fit of the nestling body condition model ($\chi^2 = 0.4$, $df = 1$, $P = 0.54$; Fig. 2D).

In the long-term data, supplementation level significantly improved the model fit for lay date ($\chi^2 = 33.5$, $df = 1$, $P < 0.001$; Fig. 3A), clutch size, ($\chi^2 = 10.0$, $df = 1$, $P = 0.002$; Fig. 3B), and brood size ($\chi^2 = 4.7$, $df = 1$, $P = 0.03$; Fig. 3C), but not for nestling condition ($\chi^2 = 1.6$, $df = 1$, $P = 0.20$; Fig. 3D). Based on the best-fitting models, females that received high levels of supplementation were predicted to lay their eggs 7.3 ± 1.2 d earlier, lay 0.2 ± 0.07 more eggs, and have 0.2 ± 0.1 more nestlings compared to females receiving low levels of supplementation.

DISCUSSION

Using both long-term data and an experimental manipulation, we provide evidence that the reproductive

performance of Gray Jays is limited by food availability. Although food limitation has been shown in species that rely on fresh food during the breeding season (Arcese and Smith 1988, Wiehn and Korpimäki 1997), our results demonstrate that caching may not always ensure adequate food supply during reproduction. This is particularly relevant in the context of Gray Jays in Algonquin Park, a population that has declined by over 50% in the past 35 years (Waite and Strickland 2006, Strickland et al. 2011). A lack of adequate food supply linked to reproductive performance could be the primary mechanism driving observed declines. Previous studies have documented a concurrent decline in reproductive success (Waite and Strickland 2006), but not in adult or juvenile survival (Norris et al. 2013) in the Algonquin Park Gray Jay population. One hypothesis to explain this decline is that warmer fall temperatures over time are increasing the spoilage of cached food, an effect that then carries over to decrease reproductive success (Waite and Strickland 2006). Our results support a major assumption of this “hoard-rot”

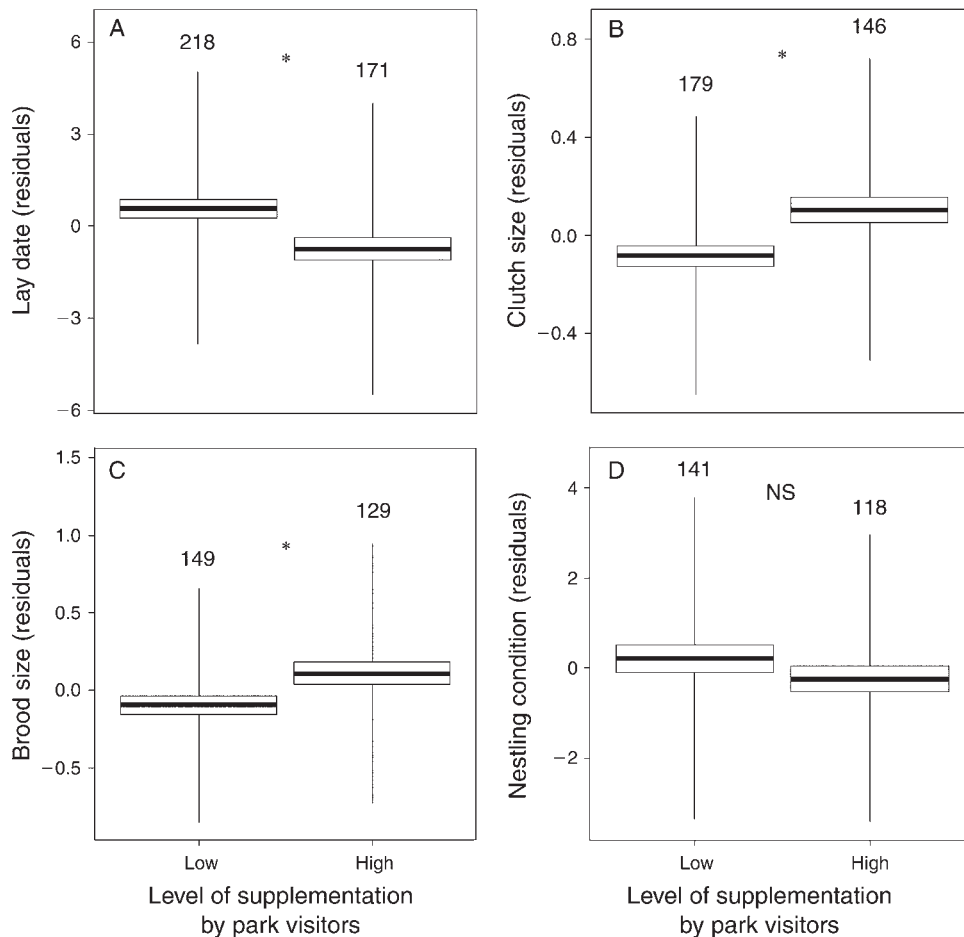


FIG. 3. Effect of food supplementation on model residuals for linear mixed-effects models that modeled the effects of female age, female identity (random effect), and year (random effect) on (A) lay date, (B) clutch size, (C) brood size, and (D) nestling condition in the long-term data set for Gray Jays in Algonquin Park, Ontario. Details of the boxplots are as in Fig. 2.

hypothesis, namely that Gray Jays are food limited during the breeding season.

One of the strongest and most consistent effects of food supplementation appeared to be on the timing of breeding. Gray Jays already begin breeding during the late winter and earlier breeding at times of high food abundance would, therefore, push individuals to nest in even colder temperatures. Strickland and Ouellet (2011) proposed that, despite cold temperatures, Gray Jays begin breeding in the late winter rather than the spring, in part because food storage and retrieval requires complex spatial memory, and it is possible that early breeding allows newly fledged young a better opportunity to properly develop this and other survival skills before the onset of the following winter. Earlier fledged young may also be more successful in competing for and securing a territory, which is critical for adequate food storage and survival during the winter months (Strickland and Ouellet 2011). Alone or in combination, these hypotheses could also explain our finding that pairs nest

even earlier in the winter when provided with supplemental food during the pre-breeding period.

Regardless of the exact mechanism favoring early nesting, an analysis of the long-term data indicates convincingly that earlier nesting leads to higher reproductive performance: in a subsequent model selection analysis using the same methods described here, we found that lay date significantly improved the fit of models to explain both the clutch size and brood size when compared to models that had only female age and supplementation level as predictor variables (likelihood ratio test; for clutch size, $\chi^2 = 47.1$, $df = 1$, $P < 0.001$; for brood size, $\chi^2 = 21.3$, $df = 1$, $P < 0.001$). Following the hoard-rot hypothesis, if warmer fall temperatures do lead to cache spoilage, it is possible that selection would be even stronger to begin nesting in the midwinter so as to avoid, what could be a very low supply of cached food during the late winter. However, we speculate that selection for nesting in the midwinter is unlikely because females would be forced to incubate in extremely cold temperatures and young presumably would be raised

under subzero conditions for most or all of the time they were in nest. Thus, although there is clearly an advantage to nestling earlier within the observed nesting schedules, there is almost certainly a threshold that Gray Jays could not cross to be able to successfully rear young.

Given the results presented here, one of the primary proximate mechanisms influencing the timing of breeding appears to be female body condition, as originally hypothesized for birds by Perrins (1970). Although we did not directly measure the body mass gain of females during the experiment, an earlier study showed that female Gray Jays, on average, gain 25% of their body mass prior to breeding and that the final mass attained by females just prior to laying influences reproductive performance (Sechley et al. 2013). These findings are similar to those from several studies of non-caching animals (Wauters and Dhondt 1989, Weimerskirch 1992), as well as of some caching birds (Hörnfeldt and Eklund 1990, Wiehn and Korpimäki 1997). It is therefore likely that supplemented female Gray Jays were able to breed earlier because they attained adequate nutritional condition sooner than did control birds.

Although we did not find evidence that clutch size was influenced by the experimental supplementation, there was an effect of visitor supplementation from the long-term data set. We see three possible explanations for this discrepancy. First, there could be a strong genetic component to clutch size (Postma and van Noordwijk 2005, Garant et al. 2008). However, it seems unlikely that we would see an effect of food on clutch size in the long-term data if this were the case, although there could be changes in the composition of genes that control clutch size or selection for changes in these gene frequencies over time. Second, it is possible that we simply did not have enough power to detect differences in clutch size in the experiment, given that there is little variation in Gray Jay clutch size (only 9.7% of clutches in this population exceeded the modal clutch size of three). Inspection of the residuals from the model without supplementation in the experimental results showed that clutch size was marginally higher in supplemented territories, suggesting that there might have been a statistically significant difference with a larger sample (Fig. 2B). Finally, we might have seen an effect only from the observational data set because visitors fed birds throughout the breeding period, whereas the experiment involved food supplementation only during the pre-breeding period. This last possibility could be the case if Gray Jays are “income” breeders, meaning that clutch size is determined by the amount of energy directly available during laying (Drent and Daan 1980, Jönsson 1997, Meijer and Drent 1999). For females that are supplemented by the public, there may be more energy available during clutch initiation through both previously stored caches and “fresh” food available from park visitors.

Although the effect of food supplementation on clutch size was not similar between the two data sets, there was a consistent effect of supplementation on brood size in both data sets. Based on the experimental supplementation that occurred during the pre-breeding period, this result suggests that pairs are able to successfully rear more young, even if the young do not receive “fresh” food at the time of chick rearing (i.e., food that was not cached and potentially affected by spoilage or robbery, thus decreasing its availability). Nevertheless, the effect of food on brood size is perhaps the strongest piece of evidence that reproductive performance in Gray Jays is food limited because, of all the variables measured, it is likely to be our best indicator of per capita recruitment.

Given the effect of food supplementation on brood size, why did we not find a similar effect on nestling body condition? One explanation is that our method of estimating body condition was not accurate because we did not know the exact age of nestlings. If nestlings were either small or large for a given age, our body condition estimate would not have reflected these differences. However, given the good fit of our model to explain age based on size (PC1) in our sample of known-age nestlings ($R^2 = 0.94$), it is likely that the PC1 values were a good estimate of age. An alternative explanation of why supplementation did not influence nestling body condition is that Gray Jays are thought to limit the amount of activity around their nest to reduce the probability of predation, primarily by red squirrels *Tamiasciurus hudsonicus* (Strickland and Waite 2001). This hypothesis has been proposed to explain why breeding pairs have extremely low nest visitation rates (achieved by bringing very large food loads) and prevent cooperative breeding before the fledgling period by chasing any 1-year-old offspring away from active nests (Strickland and Waite 2001). If there is strong selective pressure to reduce nest visits, then parents would not necessarily increase visits at higher levels of food abundance. Another alternative is that nestlings reared under limited food supply may be in good body condition because clutch sizes are lower and fewer nestlings are competing for the available food, an effect that has been observed in Eurasian Magpies *Pica pica* (Högstedt 1981).

We have also shown that regular feeding by the public can have a positive effect on reproductive performance (Robb et al. 2008). In contrast, some studies suggest that human feeding may actually have detrimental effects on bird populations, for example by decreasing brood sizes (Harrison et al. 2010), altering sex ratios (Robertson et al. 2006), and even causing nutrient limitation (Heiss et al. 2009; see Robb et al. [2008] for a review of these and other effects of food supplementation on wild bird populations). We found the opposite effect of public feeding on brood size and we are not able to test for long-term variation in sex ratios. It is possible that public feeding could lead to nutrient limitation because

many Algonquin Park visitors provide Gray Jays with bread, and if protein is limiting in wild foods, this supplement probably would not be adequate to prevent food limitation. Conversely, it is possible that calories could be more limiting than protein (Nager et al. 1997), in which case bread might actually be a valuable supplement to help prevent food limitation. Although we are not certain which nutrients are limiting in this population, we found that pairs regularly fed by the public bred earlier and raised more young than pairs not regularly in contact with the public. However, despite higher reproductive success of Gray Jays on supplemented territories, food provided by the public has been insufficient to prevent the decline of Gray Jays in Algonquin Park (Waite and Strickland 2006, Strickland et al. 2011). This may be due to the fact that the entire study area, let alone the occupied and supplemented territories, accounts for less than 2% of the park's area. We emphasize that drawing conclusions on the effectiveness of supplemental feeding requires detailed demographic data that consider multiple competing factors including the population growth rate, the effective size of the population taking into account dispersal, the specific nutrients that may be limiting in the diet, and the proportion of individuals having access to supplemental food. This is particularly relevant if supplemental feeding is proposed as a measure to increase the reproductive output of threatened or endangered species (Schoech et al. 2008).

Although our study provides strong evidence that Gray Jays are food limited during the breeding period, we acknowledge that our results may not necessarily be more broadly applicable to all food-caching species. It is possible that Gray Jays are more limited in the amount of food they are able to store than other caching species because they store only perishable items (Strickland and Ouellet 2011) and, at least in the southern portions of their range, may begin storing food only in the late summer with the arrival of cooler weather more conducive to preservation (Waite and Strickland 2006, Strickland et al. 2011). That said, species that store more rot-resistant food, such as the Florida Scrub-Jay (*Aphelocoma coerulescens*), have also been shown to be food limited during the breeding season (Schoech 1996, Reynolds et al. 2003a), so the storability of the food may not be the only factor predicting food limitation. A general understanding of food limitation in caching animals is particularly important because reproductive success in these species may be influenced not only by immediate changes in food availability during the reproductive period, but also by fluctuations in their food source during periods when they are actively caching food. Although both caching and non-caching animals often face large seasonal fluctuations in fresh food availability, caching animals can also encounter additional food shortages if caches are robbed or spoiled (Vander Wall 1990, Inman et al. 2012). Moreover, there is evidence that climate change leads to greater rates of

cache spoilage and this may lead to long-term declines in cached food availability (Waite and Strickland 2006, Strickland et al. 2011, Inman et al. 2012). Although caching may be a strategy to survive periods of food scarcity, this strategy may not prevent population declines if declines in cached food availability lead to reduced reproductive success. It will be important to understand how food limitation may influence reproductive success if we are to determine the fitness consequences of both seasonal and long-term changes in food availability.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/15-0191.1.sm>