

**Experimental evidence and over forty years of monitoring data show that food
limits reproductive success in a boreal food-caching passerine**

By

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ABSTRACT

EXPERIMENTAL EVIDENCE AND OVER 40 YEARS OF MONITORING DATA SUPPORT THE FOOD-LIMITATION HYPOTHESIS IN A BOREAL FOOD-CACHING PASSERINE

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Food caching is a unique behaviour undertaken by several species of birds and mammals to overcome periods of food scarcity, but it is virtually unknown whether caching species are food-limited. The gray jay (*Perisoreus canadensis*) is a boreal resident passerine that stores food during the late summer and fall and breeds in late winter when fresh food is scarce. Using a two-year experiment and 43 years of monitoring data, we tested the food limitation hypothesis in a declining population of gray jays in Algonquin Provincial Park, ON, Canada. Females that were supplemented both experimentally and by park visitors laid eggs earlier in the season and raised more nestlings. Females that were supplemented by park visitors also had larger clutches than non-supplemented females. Nestling condition was not influenced by food supplementation. Our results support the food-limitation hypothesis and have important implications for understanding the mechanism driving the decline in this population.

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INTRODUCTION

It is well established in a wide range of animals that reproduction is energetically costly (birds: Nur 1984, Brand and Bowman 2012; mammals: Gittleman and Thompson 1988, Key and Ross 1999; reptiles: Olsson et al. 1997; insects: Watson et al. 1998; fish: Hendry and Berg 1999; marine invertebrates: Fernández et al. 2000). High energetic demands are associated with multiple stages of the reproductive cycle, for example the production of eggs in oviparous species (Fitzpatrick 1973, Vance 1973, Tallamy and Deno 1982, Congdon 1989, Lambert and Dutil 2000, Nilsson and Råberg 2001, Vézina and Williams 2005), brooding or incubating (Fitzpatrick 1973, Vance 1973, Tallamy and Deno 1982, Fernández et al. 2000, Reid et al. 2000, Hanssen et al. 2003, Lardies et al. 2004, Reardon and Chapman 2010), gestation and lactation in mammals (Lochmiller et al. 1982, Gittleman and Thompson 1988, Mover et al. 1988, Clutton-Brock et al. 1989), and care of young until independence in altricial species (Tallamy and Deno 1982, Townsend 1986, Gittleman and Thompson 1988, Daan et al. 1990, Steinhart et al. 2005). Because of the elevated energetic demand associated with reproduction, evidence suggests that food availability can have important consequences for reproductive performance (Martin 1987). Observational studies have shown that reproductive performance in multiple taxa increases in years or territories associated with high natural food availability (Ballinger 1977, Thresher 1985, Korpimäki and Hakkarainen 1991, Deslippe and Savolainen 1994, Morrison and Bolger 2002, Boutin et al. 2006). Experimentally increasing food in animal populations has been shown to advance the timing of breeding (Hansen and Batzli 1978, Lenski 1984, Meijer et al. 1990, Reynolds et al. 2003a, Du 2006, Kerr et al. 2007), increase the number of offspring produced (Wise 1979, Högstedt 1981, Vanni 1987, Guyer 1988, Abell 1999, Reynolds et al. 2003a), improve the nutritional condition of offspring (Arcese and Smith 1988, Simons and Martin 1990,

Kreiter and Wise 2001, Jonsson et al. 2002, Gagliano and McCormick 2007, Samhuri 2009), lead to more breeding attempts (Arcese and Smith 1988, Banks and Dickman 2000, Taylor et al. 2005, Du 2006), and result in a larger number of young produced to independence (Högstedt 1981, Dhindsa and Boag 1990, Ridgway and Shuter 1994, Jonsson et al. 2002, 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 behaviour that occurs in a variety of species (Vander Wall 1990), primarily, but not exclusively, at northern latitudes (Smith and Reichman 1984). Some caching species even rely on stored food during the reproductive period (Ligon 1978, Korpimäki 1987, Vander Wall 1990, Wellicome 2005). 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 (*Aegolius funereus*) 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 (e.g. 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*), a non-migratory, food-caching passerine of North America's boreal and subalpine forests (Strickland and Ouellet 2011). Most food-caching birds store seeds or nuts which 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 sub-zero temperatures (Strickland and Ouellet 2011). In Algonquin Park, ON, 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, ON, Canada was predicted, in part, by whether females 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 females and the analysis did not account for female age or the fact that females bred over multiple years making them non-independent 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 females provided with supplemental food would have higher reproductive success,

as measured by earlier lay date, higher clutch size, more nestlings, and higher nestling nutritional condition, compared to non-supplemented females.

METHODS

Study system

We conducted our study in Algonquin Provincial Park, ON, Canada (45°33'N, 78°38'W; Fig. 1) 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 Hwy 60 corridor which transects the park and currently contains ~30 occupied territories of ~160 ha each. Gray jays in this population typically begin nesting in March, with the earliest lay date recorded in late February (Strickland and Ouellet 2011). Females produce a single brood per season, although replacement nests can be built if the first nest fails during the incubation period and early in the breeding season (Strickland and Ouellet 2011). All jays within the population are banded with a unique colour combination of three leg bands in addition to a standard Canadian Wildlife Service aluminum leg band. Individuals are banded as nestlings or when discovered as newly dispersed immigrants into the study area. Ages of the latter are estimated as juvenile (1 yr) or adult (≥ 2 yrs).

Experimental food supplementation

We conducted a food supplementation experiment during the pre-breeding period (Jan 31-Feb 26) over two years (2013, 2014). We chose to supplement female gray jays with high-protein cat food given evidence that protein influences reproductive success in birds (Beckerton and Middleton 1982, Meijer and Drent 1999, Reynolds et al. 2003a, 2003b). In 2013, we blended IAMS® Proactive Health Kitten dry kibble (Leipsic, OH, USA; 37% DM protein, 23% DM fat)

with a 1:1 ratio of water (by weight) and then partially dried it in a conventional oven or on a stovetop. The food was blended with water so we could add powdered glycine containing the heavy isotope form of nitrogen (^{15}N) 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 (Pennsauken, NJ, USA) because we determined that the consistency of this food was better suited for the addition of the powdered 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 (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 800g quantities. After drying, we estimated that the kibble contained 2494 kcal/kg and the canned food contained 1425 kcal/kg (approximately 1000g of blended food would dry down to one 800g package). Although the canned food had fewer kcal/serving than the kibble, we attempted to keep protein consistent between seasons rather than ensuring consistent caloric intake, since evidence suggests that protein is more limiting for avian reproduction than are calories (Beckerton and Middleton 1982, Meijer and Drent 1999, Reynolds et al. 2003a, 2003b). Moreover, even with the reduced calories in the canned food, the average amount of food provided to each territory in 2014 was approximately 10513 kcal, enough to ensure that the total amount supplied for the entire supplementation period was more than needed to sustain both the male and the female throughout the entire breeding season based on the estimated daily energy requirement of 47 kcal and a 90 d breeding season, assuming that all the food in the feeder was consumed by the breeding pair (Strickland and Ouellet 2011).

We supplemented 20 mated females ($n = 10$ in both 2013 and 2014) and the remaining mated females acted as controls ($n = 13$ in both 2013 and 2014). Supplemental food was provided to females using feeders that were designed to minimize the access of other animals 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 x 12.0 mm glass tags, #601201; Cyntag®,Cynthiana, KY, USA). Feeders were made from wood and measured 30 cm high x 30 cm wide x 40 cm long. The supplemented food was placed inside the feeder at its solid rear wall, forcing the jays to enter the feeder to obtain food. We also covered the food with a layer of wire mesh to prevent smaller mammals such as American martens (*Martes americana*) and red squirrels (*Tamiasciurus hudsonicus*) from retrieving large amounts of food if they did gain access to the inside of the feeder. Feeders were hung above the ground and a minimum of ~2 m from the trunks of trees to further minimize access by mammals. Bars around the outside of the feeder prevented larger birds, such as common ravens (*Corvus corax*), from entering. We placed the feeders well inside each treatment territory (mean size of territories: 160 ha; Strickland and Ouellet 2011) to prevent jays in adjacent territories from accessing the food. Each feeder was checked daily and re-filled with 800g of food if it was more than half empty.

A thin wire antenna was placed across the front of the feeder and connected to a RFID reader placed underneath the feeder (Fig. 2A). Bars along two sides of the feeder were intentionally spaced sufficiently close together that jays were forced to enter through the front and cross the antenna by walking or hopping. RFID tags were affixed to each supplemented female by gluing the tag onto existing leg bands and then wrapping the tag with clear, waterproof tape (tesa® tape, Charlotte, NC, USA; Fig. 2B). The wire antenna was able to detect tags within ~10 cm above the horizontal antenna, and the RFID reader recorded each time a female entered

the feeder and thus allowed us to confirm that treatment females were indeed retrieving supplemented food. The RFID reader and antenna were connected to a battery source which was also placed underneath the feeder. In 2013, 9V lithium-ion batteries (Energizer®, Walkerton, ON, CAN) were used and changed daily. In 2014, 12V lead-acid batteries (Power Sonic®, Fort Worth, TX, USA) were used and changed every 3-4 days. Unfortunately, in 2013, cold weather unexpectedly reduced battery life, which meant that readers were not running continuously throughout the day. However, the readers were running for enough time each day (mean running time/feeder/d = 5 hrs, 50 min) that we could estimate the number of days that the female entered the feeder. In 2014, we also estimated daily feeding rate because improved battery life allowed for continuous operation of the RFID readers throughout the day. We estimated feeding rate as the total number of RFID fixes per day divided by two, since we assumed that the tag was recorded when the female was both entering and leaving the feeder. For logistical reasons, we did not attach RFID tags to males or juveniles so we could not estimate the proportion of food that was taken by the focal female versus other jays occupying the same territory. RFID tags were also not attached to control females, although some 2014 control females had been supplemented in 2013 and retained their tags from the previous year.

After supplementation, we tracked the reproductive performance of females on both supplemented and control territories. Measured or estimated reproductive variables were: lay date, clutch size, number of nestlings, and nestling condition (mass given body size, see below for more details). Since females rarely leave the nest once they have laid the first egg (Strickland and Ouellet 2011), lay date was 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). Since

incubation lasts 18 days (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 3 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. Once nestlings were approximately 11 d old, the nest was accessed using a ladder (if < 9 m high) or by employing 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 (2013: n = 16 nests, nestling age range when accessed: 7-12 d; 2014: n = 15 nests, age range when accessed: 8-14 d). Nestlings and unhatched eggs were then counted. In all but 3 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 number of nestlings 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 31 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).

Two supplemented territories were excluded from analysis because the female did not breed (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). 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.

Long-term data: supplementation by the public

We used data collected from 1970-2012 to examine the reproductive performance of uniquely banded females that nested on territories that were regularly supplemented by the public (park visitors) versus those not supplemented by the public. Gray jays readily seek and accept food from humans during the fall and winter when fresh food is not readily available. Because our study site generally runs parallel the main highway (Hwy 60) through the park, several monitored territories contained trail heads or other facilities heavily used by park visitors while 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 1970-2012 as having either a ‘low’ or ‘high’ level of supplementation. 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). We considered territories to have a high level of supplementation (n = 14 territories, 63 females, 172 nests) if there was either a permanent feeder, or visitors were commonly observed in both the fall and the winter feeding jays. Territories were deemed to have a low level of supplementation (n = 26 territories, 64 females, 218 nests) if they were far from roads or walking trails and rarely, if ever, accessed by the public. One territory was designated as receiving low levels of supplementation until 1992, when the current Visitor Centre was built and the territory was re-classified as receiving high levels of supplementation. If a nest failed, we did not include it in models to explain clutch size or number of nestlings (n = 66 nests) and, in some cases (n = 131 nests), not all nestling morphometric data were taken, so we could not estimate nestling condition (see below for calculations).

Statistical methods: estimating nestling condition

To estimate nestling condition, we implemented the following two steps: 1) calculated principal first component scores (PC1) from multiple morphological measurements of known-age nestlings and then examined whether these scores were an accurate reflection of age; 2) modeled the relationship between weight and PC1 scores of known-age nestlings and then used the residuals from this model to generate an estimate of condition (mass given body size) for unknown-age nestlings.

We used data from known-age nestlings collected between 1979-2012 ($n = 26$ nests, $n = 77$ nestlings). Most of these known-age nestlings ($n = 51$) were weighed every day from hatch date until a mean of 16 days of age (range = 12-21 d). However, some known-age nestlings were only weighed once ($n = 26$). For step 1, we used measurements of beak length, tarsus length and 7th primary length from all known-age nestlings to conduct a principal component analysis (Dunteman 1989), where the first principal component score (PC1) explained 94% of the variance and PC1 had strong positive loadings for all three morphological measurements (beak length = 0.59, tarsus length = 0.58, 7th primary = 0.57). The PC1 scores explained 94% of the variation in age at banding for known-age nestlings (age range: 4-12 d, $R^2 = 0.94$, $b = 2.37$, $p < 0.0001$, $n = 417$) and thus, we considered PC1 scores a good estimate of nestling age.

To select the best model for the relationship between weight and size (step 2), PC1 scores of all nestlings from the long-term (including the known-age nestlings) and experimental datasets were then calculated so that any models generated with the known-age data would be scaled properly to the PC1 scores of all nestlings in both datasets. Then, the revised PC1 scores of only the known-age nestlings were plotted against weight (Fig. 3). To select the best-fitting model for this relationship, we used Akaike Information Criteria model selection scores for small sample

sizes (AIC_c; Burnham and Anderson 2002) to test three competing models: a power function, an exponential model, and an asymptotic exponential model. Each of these models can be used to describe biological relationships, including allometric scaling relationships and growth (Logan 2010). Based on AIC_c, the best-fitting model was an asymptotic exponential model (nestling weight ($\ln(g)$) = $a+b*\exp(c*PC1 \text{ score})$; $a = 4.35$, $b = -3.23$, $c = -0.38$; Table 1). We considered the residuals from this asymptotic exponential function as the estimate of condition (mass given body size) for unknown age nestlings (Schulte-Hostedde et al. 2005, Harms et al. 2010).

Statistical methods: reproductive success

To understand how food availability influenced reproductive success, we constructed a series of linear mixed effects models 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, number of nestlings, 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 ID* and *year* as random effects. Female age was included in all models because previous evidence suggests that reproductive success increases with age (Strickland et al. 2011, Sechley et al. 2013). We included female ID 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 which may have influenced food availability and reproductive success. We then removed supplementation level from each global model to generate a second set of models for each response variable with only female age, female ID and year as independent variables in the models. 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. All statistical tests were done using R 3.0.1 (R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

For the experimental feeders in which the RFID readers worked for a minimum of 25 d of the 27 d supplementation period (2013: n = 4; 2014: n = 5), females entered a mean of 13 ± 2 d (range 4-22 d). For feeders in which we could record reliable visitation rates within a day (n = 9 feeders), females entered an average of 36 ± 8 times/day (range 2-73).

Experimental supplementation significantly improved the model fit to explain lay date ($\chi^2 = 20.9$, df = 1, $p < 0.0001$; Fig 4A), and the model predicted that supplemented females would lay eggs 8.9 ± 1.7 d 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 4B) but it did significantly improve the model fit for the number of nestlings raised ($\chi^2 = 5.3$, df = 1, $p = 0.02$; Fig 4C). Experimentally supplemented females were predicted to raise 0.7 ± 0.3 more nestlings than controls. Supplementation did not significantly improve the fit of the nestling condition model ($\chi^2 = 0.4$, df = 1, $p = 0.54$; Fig 4D).

In the long-term data, supplementation level significantly improved the model fit for lay date ($\chi^2 = 33.6$, df = 1, $p < 0.0001$; Fig 5A), clutch size, ($\chi^2 = 11.3$, df = 1, $p = 0.0008$; Fig 5B) and number of nestlings raised ($\chi^2 = 5.8$, df = 1, $p = 0.02$; Fig 5C) but not for nestling condition ($\chi^2 = 1.6$, df = 1, $p = 0.20$; Fig 5D). Based on the best fitting models, females that received high levels of supplementation from park visitors were predicted to lay their eggs 7.3 ± 1.2 d earlier,

lay 0.2 ± 0.07 more eggs, and have 0.3 ± 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 (e.g. Arcese and Smith 1988, Wiehn and Korpimäki 1997, Dewey and Kennedy 2001), our results demonstrate that food-caching is a strategy that may not always ensure adequate food supply during the reproductive period. 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 the decline of gray jays in Algonquin Park is that warmer fall temperatures over time are increasing the spoilage of cached food, an effect which then carries over to decrease reproductive success (Waite and Strickland 2006). Our results support a major assumption of this ‘hoard-rot’ 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. This is quite interesting given that 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 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 the following winter (Strickland and Ouellet 2011). Alone or in combination, these hypotheses could also explain our finding that females nest even earlier in the winter when provided with supplemented food during the pre-breeding period. Regardless of the exact mechanism favouring 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 above, we found that lay date significantly improved the fit of models to explain both the clutch size and number of nestlings when compared to models that just had female age and supplementation level as predictor variables (likelihood ratio test; clutch size: $\chi^2 = 41.9$, $df = 1$, $p < 0.0001$, number of nestlings: $\chi^2 = 42.9$, $df = 1$, $p < 0.0001$).

Given the results presented here, one of the primary proximate mechanisms influencing the timing of breeding appears to be female condition, as originally hypothesized for birds by Perrins (1970). Although we did not directly measure the mass gain of females during the experiment, an earlier study showed that female gray jays gain 25% of their body weight prior to breeding and that the final weight attained by females just prior to clutch initiation influenced reproductive performance (Sechley et al. 2013). These findings are similar to those from several studies on non-caching animals (Fritz and Morse 1985, Wauters and Dhondt 1989, Weimerskirch 1992), as well as on some caching birds (Wiehn and Korpimäki 1997, Hörnfeldt and Eklund

1990). It is therefore likely that supplemented female gray jays were able to breed earlier because they attained adequate nutritional condition sooner than controls.

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 dataset. We see three possible explanations for this discrepancy. First, there could be a strong genetic component to clutch size (Sheldon et al. 2003, 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 there might have been a statistically significant difference with a larger sample (Fig. 4B). Finally, we might have seen an effect only from the observational dataset 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 (Meijer and Drent 1999, Houston et al. 2007). In the case of females that are supplemented during both the pre-breeding and breeding stages, there may be a larger amount of 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 consistent between the two datasets, there was an effect of supplementation on number of nestlings in both the experimental and long-term data. Based on the experimental supplementation that occurred during the pre-breeding period, this result suggests that females 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 the number of nestlings is perhaps the strongest piece of evidence that reproductive performance in gray jays is food-limited because, of all the reproductive variables measured, this is likely the best measure of reproductive success since it is the variable measured at the end of the nesting period and is, therefore, the best indicator of per capita recruitment. Anecdotal evidence also suggests food may influence offspring recruitment: of 56 nestlings that were banded in 20 nests in the late winter of 2013, only three were found on the study site the following fall, all of which were from supplemented territories (two experimentally and the other by park visitors).

Given the effect of food supplementation on the number of nestlings raised, why did we not find a similar effect on nestling condition? One explanation is that our method of estimating 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 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 ($R^2 = 0.94$), we are confident that the morphological measurements were a good estimate of age. An alternative explanation of why supplementation did not influence nestling condition is that gray jays are thought to limit the amount of activity around their nest to reduce the probability of predation (Strickland and Waite 2001). This

hypothesis has been proposed to explain why jays temporarily chase 1-year old offspring away from the immediate nest area during the nest-building, incubation and nestling periods, but tolerate their presence and facultative allofeeding contributions in the fledgling period (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. Since jays already carry a large food load to the nest on each trip (Strickland and Waite 2001), they also likely do not increase food loads in response to increased food availability. Lastly, the nestlings that are reared successfully under limited food supply may be in good nutritional condition because clutch sizes are lower and therefore fewer nestlings are competing for the available food, an effect that has been observed in magpies (*Pica pica*) that were experimentally food supplemented (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). 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 most visitors to Algonquin Park feed bread to gray jays, which almost surely does not have the same nutrient value as wild food. Nevertheless, we found that females regularly fed by the public bred earlier and raised more young than females not regularly in contact with the public. However, it is important to note that, despite higher reproductive success of gray jays on food-supplemented territories, it does not appear that supplemental food provided by the public has been sufficient to stem the continued decline of

gray jays in Algonquin Park (Waite and Strickland 2006, Strickland et al. 2011). This may be due to the fact that most of the territories in the study area have not historically received ‘high’ levels of supplementation, and the large size of the study area means that even high levels of supplemental feeding in a relatively small proportion of the territories in Algonquin Park did not have a population-wide effect. Thus, we emphasize that drawing conclusions on the effectiveness of supplemental feeding by the public requires detailed demographic data that takes into account multiple competing factors influencing population growth rate, the effective size of the population taking into account dispersal, and the number of individuals which have access to the 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 generalizable 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 (less boreal) 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 do store non-perishable 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 since 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. While 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, Suhonen et al. 2007, Inman 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 in the face of long-term environmental change 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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TABLES AND FIGURES

Table 1. Log-likelihood (LgL), Akaike Information Criteria model selection scores for small sample sizes ($AICc$), $\Delta AICc$, and Akaike weights ($AICcw$) for model competition between three different models used to explain nestling growth rate. 417 measurements of weight (g) and first principal component scores (PC1) of tarsus length (mm), seventh primary length (mm) and beak length (mm) from 77 nestlings in 26 nests were plotted, and the following models fit to this relationship. Models are listed in order from best to worst fit based on $\Delta AICc$

| Model | LgL | $AICc$ | $\Delta AICc$ | $AICcw$ |
|------------------------|-------------------------|--------------------------|---------------------------------|---------------------------|
| Asymptotic exponential | 405.98 | -803.87 | 0.00 | 1.00 |
| Power | 371.20 | -763.34 | 67.53 | 0.00 |
| Exponential | 262.46 | -518.87 | 285.00 | 0.00 |

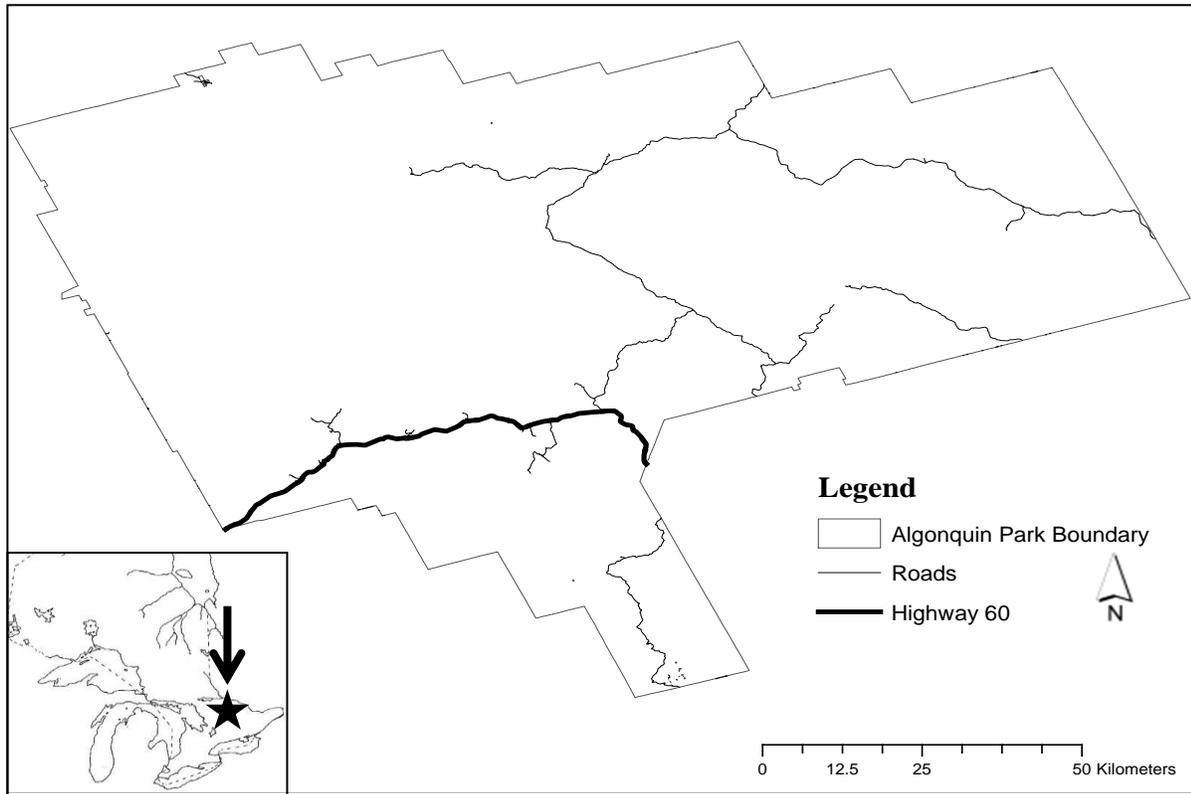


Figure 1. Map of study area and its location within Ontario (star in the inset map). The study area includes mostly coniferous-dominated areas within approximately 3 km of the Hwy 60 corridor that runs through the park and some of its associated roads.



Figure 2. Feeder design for the food supplementation experiment. A) shows a gray jay about to exit the feeder with supplemented food in its bill. 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) shows the white RFID tag attached to the leg bands on the right leg of the female (indicated by the arrow).

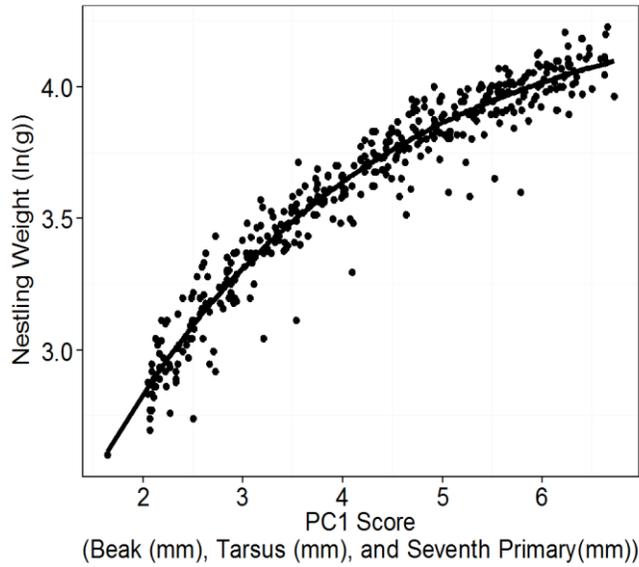


Figure 3. Log-transformed weight (g) of known-age nestling gray jays plotted against size, estimated from the first principal component score (PC1) of beak length (mm), tarsus length (mm), and seventh primary length (mm). The asymptotic exponential line represents the best fitting model from Table 1.

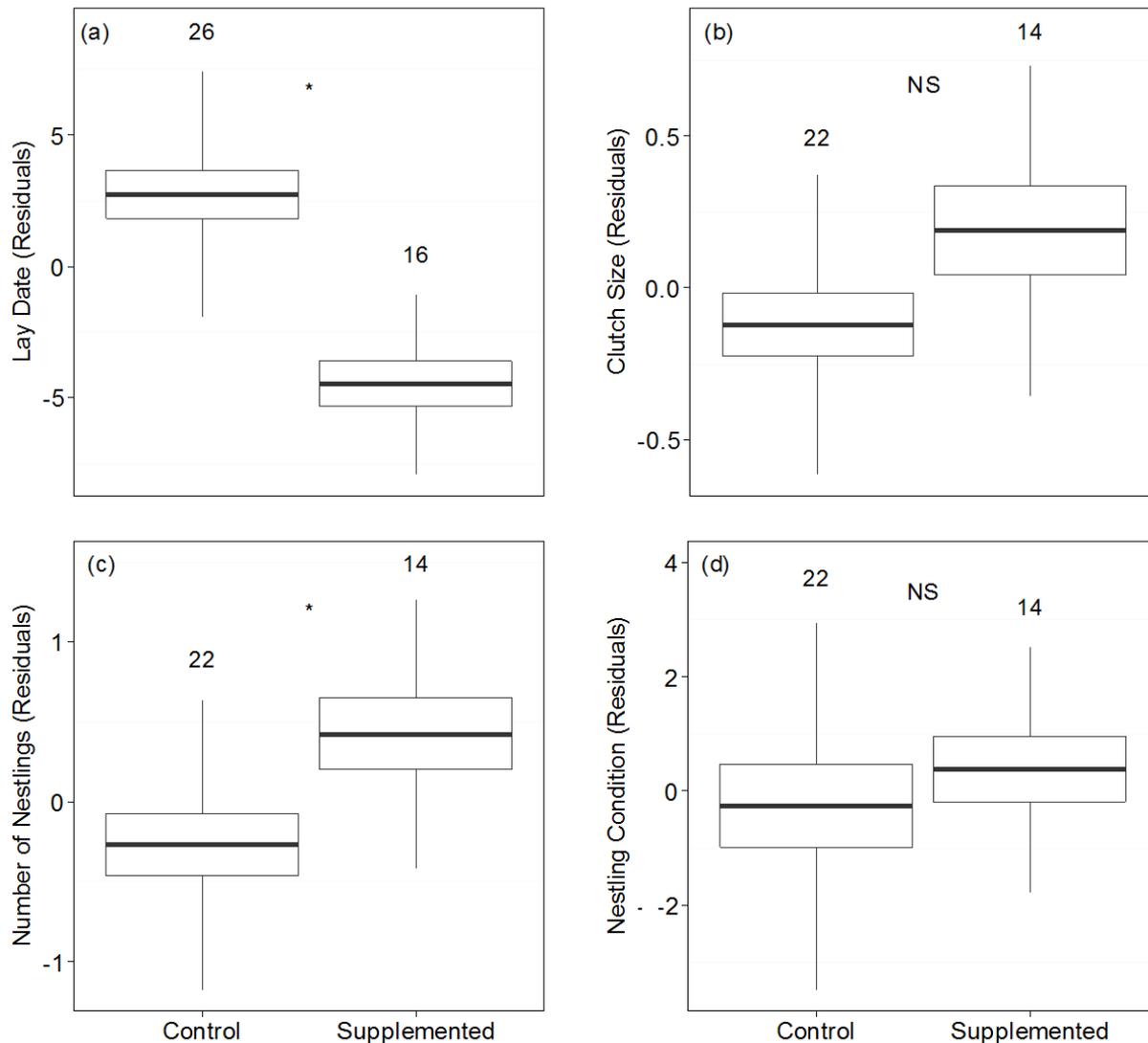


Figure 4. Experimental effect of food supplementation on model residuals for linear mixed effects models which modelled the effects of female age, female ID (random effect), and year (random effect) on A) lay date, B) clutch size, C) number of nestlings and D) nestling condition for gray jays in Algonquin Park, ON. The thick line within each box represents the mean, while 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, while ‘NS’ indicates non-significance. Supplementation

significantly improved model fit for lay date and number of nestlings but not clutch size or nestling condition.

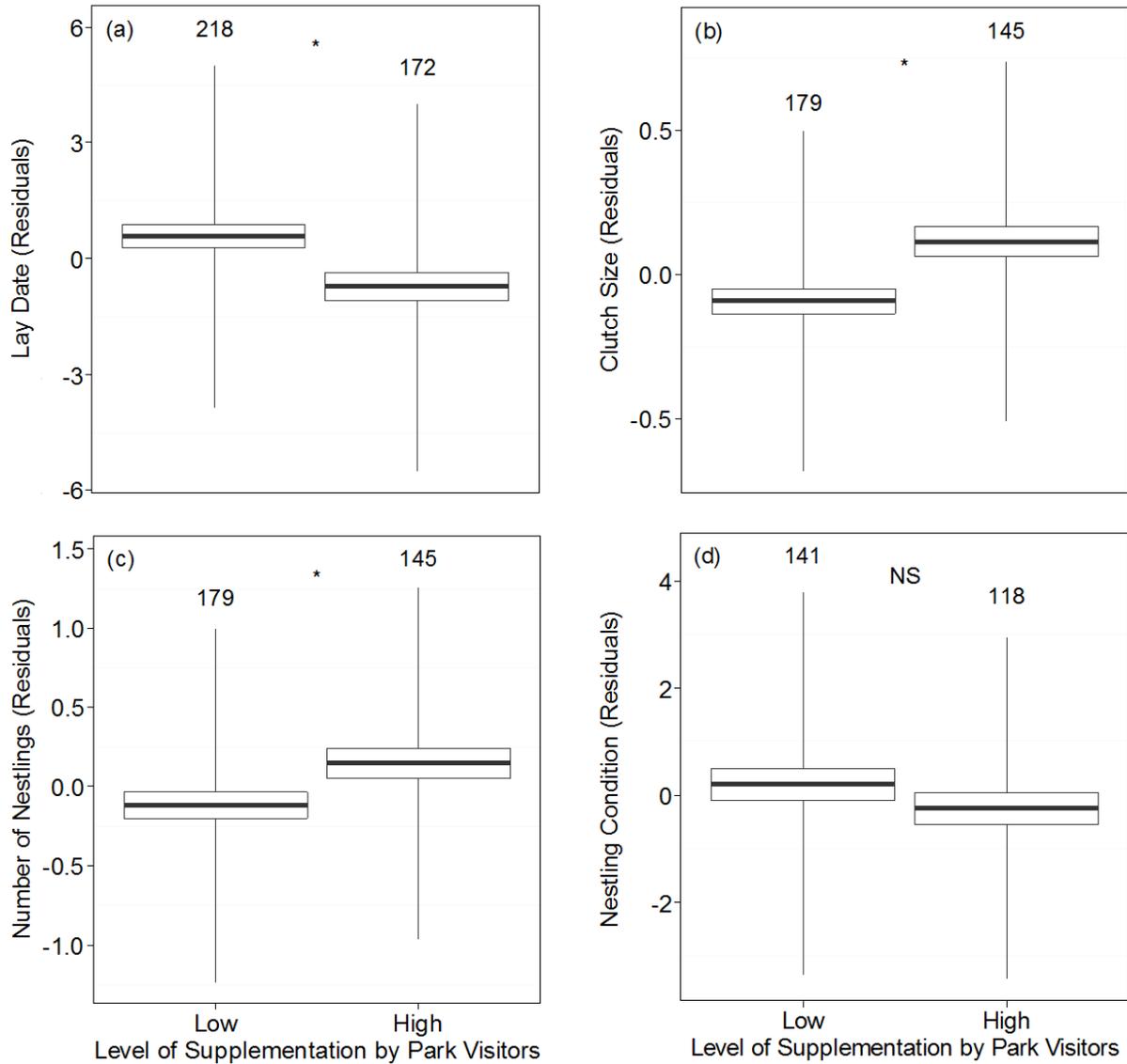


Figure 5. Effect of food supplementation on model residuals for linear mixed effects models which modelled the effects of female age, female ID (random effect), and year (random effect) on A) lay date, B) clutch size, C) number of nestlings, and D) nestling condition in the long-term data set for gray jays in Algonquin Park, ON. Box plots are the same as Fig. 3. Supplementation significantly improved model fit for lay date, clutch size, and number of nestlings, but not for nestling condition.

APPENDIX

Table A-1: Female ID, female age, and treatment (supplemented or control) for each territory occupied by a breeding pair during the 2013/2014 food supplementation experiment. A ‘+’ symbol next to the age indicates a minimum estimated age for females that were banded as immigrant adults. In 2013, ‘Alligator’ and ‘Sunday Creek’ were excluded from the analyses because they were supplemented territories but the females never entered the feeders. ‘Davie’s Bog’ was excluded in 2013 because the female did not breed (there was no breeding male) and excluded in 2014 because the territory was supplemented but the female never entered the feeder. ‘Cameron Lake Road’ was excluded in both years because it was already heavily food supplemented by park visitors.

| Territory Name | Female ID 2013 | Female Age 2013 | Treatment 2013 | Female ID 2014 | Female Age 2014 | Treatment 2014 |
|-----------------------|-----------------------|------------------------|-----------------------|-----------------------|------------------------|-----------------------|
| Alligator | LOYLOOSR | 4 | -- | LOYLOOSR | 5 | Control |
| Arowhon | YOSLYOKR | 2+ | Control | YOSLYOKR | 3+ | Control |
| Arowhon East | GOSLPOOR | 6+ | Control | -- | | -- |
| Bat Lake | TOSLLOOR | 11+ | Supplemented | -- | | -- |
| Big Pines | BOGLWOSR | 8 | Supplemented | BOGLWOSR | 9 | Control |
| Boardwalk | TOKLGOSR | 2 | Control | TOKLGOSR | 3 | Supplemented |
| Cameron Lake Road | KOOLOSR | 6+ | -- | KOOLOSR | 7+ | -- |
| Cedar Swamp | GOSLBOLR | 2 | Control | GOSLBOLR | 3 | Supplemented |
| Clarke Lake | LOSLWOYR | 1 | -- | LOSLWOYR | 2 | Control |
| Cliff | POSLKOTR | 1 | Control | POSLKOTR | 2 | Supplemented |
| Crossroads | -- | | -- | POSLROYR | 1 | Control |
| Davie’s Bog | OOSLBOGR | 6+ | -- | OOSLBOGR | 7+ | -- |
| Duck East | BOKLWOSR | 1 | Control | -- | | -- |
| Hermit Creek | -- | | -- | YOSLBOBR | 2 | Control |
| Mad Rock | BOYLROSR | 5+ | Control | BOYLROSR | 6+ | Control |
| Mile 36 | LOSLTOBR | 9 | Supplemented | GOSLKOOR | 2 | Control |

| | | | | | | |
|----------------|----------|-----|--------------|----------|-----|--------------|
| North Bog | OOSLPOLR | 7+ | Control | OOSLPOLR | 8+ | Supplemented |
| Opeongo Bridge | POOLYOSR | 11+ | Supplemented | POOLYOSR | 12+ | Control |
| Opeongo Turn | GOSLYOYR | 1+ | Control | GOSLYOYR | 2+ | Supplemented |
| Rock Yard | YOYLYOSR | 4+ | Supplemented | YOYLYOSR | 5+ | Control |
| Sim's Pit | POLLWOSR | 2 | Supplemented | KOYLYOSR | 1 | Supplemented |
| Sunday Creek | KOSLBOYR | 2 | -- | KOSLBOYR | 3 | Control |
| SW Airfield | ROSLLOYR | 5+ | Control | GOSLWOKR | 1 | Control |
| TDS North | POYLTOSR | 9 | Control | POYLTOSR | 10 | Supplemented |
| TDS South | OOLLROSR | 5+ | Supplemented | OOLLROSR | 6+ | Control |
| Track | -- | | -- | WOLLLOSR | 2+ | Supplemented |
| Wolf Howl Pond | OOSLROOR | 2 | Control | OOSLROOR | 3 | Supplemented |
| Wood Duck | WOKLBOSR | 2 | Control | WOKLBOSR | 3 | Control |