Articles

Causes and consequences of pre-laying weight gain in a food-caching bird that breeds in late winter

Talia H. Sechley, Dan Strickland and D. Ryan Norris

T. H. Sechley (tsechley@uoguelph.ca), and D. R. Norris, Dept of Integrative Biology, Univ. of Guelph, Guelph, ON N1G 2W1, Canada. – D. Strickland, 1063 Oxtongue Lake Road, Dwight, ON P0A 1H0, Canada.

Animals that reside at high latitudes and altitudes year-round often use cached food to survive over the winter months, but a few species also rely on stored food to sustain them during the breeding season when the nutritional requirements of females are higher than normal. Gray jays *Perisoreus canadensis* rely on perishable cached food during the winter and females begin breeding in late winter when fresh food is rarely available. To examine pre-laying patterns of weight gain, as well as the causes and consequences of weight gain among individuals, we weighed females regularly throughout the pre-laying period. Females began increasing their weight approximately nine days prior to their first egg date, and on average increased their body weight by 25%, which is on par with other bird species that rely on non-cached food. Final pre-laying weight was positively influenced by the percent of conifers on territories, providing some support for previous results showing that coniferous trees are better able to preserve cached food. We also found that both final pre-laying weight and the rate of weight gain were positively related to female age, supporting the hypothesis that female caching ability improves with age. With increasing final weight, females tended to lay larger clutches and hatched more nestlings, despite the fact that final weight was not influenced by weight at the beginning of the weighing period. Our results confirm that gray jays are able to reach breeding condition while relying primarily on food stored before winter, and suggest a novel mechanism by which habitat-mediated carry-over effects and female age may influence reproductive performance in a food-caching animal.

Hoarding behaviour evolves when food sources are scarce or unreliable at certain times of the year or when harsh climatic conditions preclude access to food (Sherry 1985, McNamara et al. 1990, Vander Wall 1990, Pravosudov and Grubb 1997). Birds and mammals that permanently reside in boreal environments often rely on cached food to fulfill their nutritional requirements during the winter months (Smith and Reichman 1984, Vander Wall 1990, Pravosudov and Lucas 2001). Moreover, a subset of boreal food-hoarders rely on stored food, not only for over-winter survival but also to meet the nutritional demands imposed by their late-winter breeding seasons (e.g. wolverine *Gulo gulo*: Persson 2005; gray jay *Perisoreus canadensis*: Strickland and Ouellet 2011; red squirrel *Tamiasciurus hudsonicus*: Fletcher et al. 2013).

In non-caching birds, several studies have shown that females gain weight rapidly prior to laying (Newton et al. 1983, Ojanen 1983, Hohman 1986), and both the rate and amount of weight gained can influence breeding performance (Ankney and MacInnes 1978, Drobney 1982, Newton and Marquiss 1984, Woodburn and Perrins 1997). Females have been shown to advance their timing of breeding and produce larger clutches when they are provided access to supplemental food during the pre-laying period

(Newton and Marquiss 1981, Arcese and Smith 1988, Schoech 1996). We address the question of whether similar patterns of spectacular weight gain and breeding performance are seen in cache-dependent, late-winter-breeding boreal birds. Although some weight gain is required in order for females to produce eggs, a marked increase in weight prior to breeding would be noteworthy in these potentially food-limited species, given that food stores will have necessarily been diminished by several months of over-winter consumption by the breeders themselves and possibly both conspecific and heterospecific competitors as well. A dramatic increase in female weight prior to laying would suggest that females accumulate fat and protein stores prior to producing eggs, much like the traditional notion of a capital breeder (Drent and Daan 1980).

In this study, we set out to examine patterns of weight gain during the pre-laying period (early February to mid-March) in female gray jays *Perisoreus canadensis*. Gray jays are sedentary residents in North American boreal and sub-alpine forests and are scatter hoarders, meaning that they cache thousands of items separately throughout their territory (Vander Wall 1990). Caches are coated with sticky saliva and then typically wedged under bark scales or arboreal lichens (Dow 1965). Gray jays cache food during

the late summer and fall and, unlike most other caching birds, store exclusively perishable food (e.g. berries, fungi, arthropods, carrion; Strickland and Ouellet 2011). In addition, females initiate clutches as early as late February in our southern study area when temperatures are well below freezing and snow depths may surpass 1 m. Fledging occurs in late April–early May when > 90% of local migratory passerines have not returned, let alone commenced breeding themselves (Strickland and Ouellet 2011). Thus, females must also rely on cached food during the pre-laying, laying, and incubation periods and, at least partially, when feeding nestlings in April (Strickland and Ouellet 2011).

Although gray jays breed under severe conditions, we hypothesized that pre-laying female weight gains would be comparable to those reported in species that rely on fresh food because female gray jays are still faced with the same or even greater nutritional demands for breeding. This hypothesis was based on two past observations from our long-term study. First, two females banded in the pre-laying period weighed more than any known male even though outside the breeding season, males are on average 12% heavier than females (75.7 ± 3.0 g, mean ± SD vs 67.5 ± 3.0 g; Strickland and Ouellet 2011). Second, a single female baited to an electronic scale showed a 29% increase in weight in ten days just prior to initiating a clutch while the weight of her male partner remained constant (Strickland unpubl.).

We also examined the causes of variation in the rate of weight gain and final weight prior to laying eggs. Since we found that 'final weight' (measured 1 d prior to clutch initiation) was not related to the rate of weight gain, we examined both of these variables separately. Previous evidence has shown that simulated caches of mealworms, raisins and blueberries lost less weight over 1–5 months when artificially stored on coniferous trees compared to deciduous trees and that gray jays occupying territories with a low percentage of conifers had lower reproductive success than jays occupying territories with a high percentage of conifers (Strickland et al. 2011). This suggests that habitat quality is in part driven by the superior ability of conifers to preserve food that is cached before winter, which then carries over to influence breeding success several months later. Following this carry-over effect hypothesis, we predicted that females occupying territories with a higher percentage of conifers would gain weight at a faster rate (due to the potential costs of being fat for a longer period of time: Lima 1986, McNamara et al. 1990, Gosler et al. 1995) and would attain a higher final weight (due to the potential advantages of having more fat reserves for egg laying: Newton et al. 1983, Perrins 1996, Woodburn 1997) compared to females in territories with a lower percentage of conifers. Age may also play a role in the pre-laying weight gain in females that rely on cached food. Studies have shown that age influences the ability of corvids to successfully retrieve cached items because the process largely relies on memory formation and learned behaviours (Bunch and Tomback 1986, Clayton 1998, Dally et al. 2006). Following this caching experience hypothesis, we predicted that the rate of weight gain and the final weight of females both increase with age.

Finally, we examined how variation in weight gain could influence reproductive performance. Following previous work on non-caching songbirds (Houston et al. 1995, Perrins 1996, Siikamäki 1998), we hypothesized that the final weight of females prior to first egg would influence the timing of laying and reproductive success, since heavier birds will have accumulated a greater amount of reserves with which to form the clutch. We also hypothesized that the timing of laying and reproductive success would be influenced by the rate of weight gain, since females that are proficient in caching and retrieving cached food may be able to gain weight rapidly when laying conditions are ideal, in order to avoid having a high body weight for a prolonged period of time. We predicted that females exhibiting higher rates of weight gain and higher final weights would initiate clutches earlier. We also predicted that rate of weight gain and final weight would be positively related to clutch size, the number of hatched nestlings, nestling condition, and the probability of successfully fledging young.

Methods

Field methods

Fieldwork was carried out in Algonquin Provincial Park, Ontario, Canada (45°33′N, 78°38′W), where a marked gray jay population has been monitored since the mid 1960s along the Highway 60 corridor in the southwestern portion of the park (Rutter 1969, Strickland 1991, Strickland and Waite 2001). All birds in the study population were identifiable by a unique combination of up to three coloured leg bands and one standard Canadian Wildlife Service aluminum leg band. During the 2012 breeding season (February–May), data on weight gain and reproductive success were collected from 22 territories. Each territory (mean size: 160 ha; Strickland and Ouellet 2011) was occupied by a pair of mated adults. In 10 cases, a 1- or 2-yr old non-breeder that was a philopatric offspring or a year-old immigrant was also present, and in two cases, two non-breeders were present. Non-breeders sometimes feed their younger siblings but only during the fledgling period, indicating that gray jays exhibit limited alloparental behaviour (Waite and Strickland 1997, Strickland and Waite 2001). The percent of conifers within each territory was used as an index of territory quality (see Strickland et al. 2011 for rationale and methods). Two territories recently added to the study area were omitted from this analysis in our current study because we did not have conifer data for them comparable in quality to those used to estimate percent conifers in our previous study (Strickland et al. 2011).

Between 13 February and 30 March, we used a remote weighing system to weigh males and females throughout the pre-laying period. The remote weighing system consisted of an electronic balance modified by the addition of a 10 cm tall plastic container to the pan, on top of which we secured a small block of cheese with rubber bands. The plastic container was used to elevate the jays enough to prevent their tail from touching the side of the scale or the snow beside the scale. Gray jays typically remained on the scale pecking at the cheese and accumulating a bolus for subsequent storage long enough that we could obtain a weight reading. Output from the screen of the electronic balance and the colour bands of the bird were recorded using a video camera attached to

a tripod. Video recordings generally lasted for 3–5 min for each pair and were played back later to estimate jay weights to the nearest 0.1 g (when the bird settled down on the scale and the output remained constant for 3–4 s). The accuracy of the weighing system was assessed by comparing the weights of 12 birds (7 females, 5 males) obtained from the remote weighing device to those obtained immediately afterwards by capturing the same birds in a walk-in trap and weighing them using a Pesola scale. The weights based on the two measurement techniques were highly correlated (Pearson product-moment correlation coefficient, r = 0.99, n = 12, p < 0.0001). Very few weights were obtained after clutch initiation because, although true incubation in the gray jay normally starts with the laying of the last egg, females sit on the nest beginning with the first egg (Strickland and Ouellet 2011) and they could not often be enticed to leave even an incomplete clutch.

The first female to lay eggs did so 15 d after we began weighing her, so the initial pre-laying weight for all females (hereafter called 'initial weight') was defined as weight 15 d before first egg. Similarly, the 'pre-laying period' was defined as the 15 d prior to first egg date. Although some females that laid later in the season were weighed up to 30–40 d prior to first egg, average female weight 15 d prior to first egg (67.2 ± 3.1 g) was not significantly different than female weight 15–40 d prior to first egg (66.7 ± 3.0 g; Student's paired t-test: $t_{19} = -1.10$, p = 0.28), suggesting that our initial weight measurement at 15 d prior to first egg still captured the initial (or baseline) weight of females. We defined 'final weight' as the weight measurement taken from females one day prior to the date they laid their first egg. In four cases, we were unable to obtain female weights on the day prior to first egg so the final weights for these females were estimated from the curve fit based on the rate of weight gain. We considered the 'beginning of weight gain' the day the female gained ≥ 2 g in relation to her initial weight, and this variable was used to examine the relationship between the timing of exponential weight gain and first egg date. The calculation for 'rate of weight gain' is described below. Since we did not expect male weights to change as a direct result of preparing to breed, we used male weights as a 'control'. Males were measured at the same time (i.e. same 3–5 min video session) as their female partners. Although we attempted to weigh each pair at least every other day for 15 d prior to incubation, occasionally we could not locate pairs on their designated weighing day and the pair would therefore be weighed on the following day.

Nests were found during the nest-building period by supplying jays with nest material (teased-apart cotton balls and, in late stages of nest construction, contour feathers of ruffed grouse *Bonasa umbellus*) and then following them to their nest site. Two nests were found during the incubation stage. Nests were checked every 1–2 d, which allowed us to determine the 'first egg date' for females within the study area. Hatching was assumed to be complete 20 d after the initiation of a 3-egg clutch (Strickland and Ouellet 2011). 'Clutch size' was observed directly (by mirror-pole) in nests lower than 6 m and, for higher nests, estimated by adding the number of nestlings to the number of un-hatched eggs (if any) in the nest at the time of banding. Nests were accessed for this purpose between 9–13 d post-hatch by

ladder or, for nests above 10 m, by a professional arborist. As with adults, nestlings were banded with a unique combination of three colour bands and a Canadian Fish and Wildlife Service aluminum leg band, weighed to the nearest 0.1 g using a Pesola scale, and beak, tarsus, 7th primary and tail length measurements were taken. 'Nestling condition' was estimated by comparing the observed weight at banding to their expected weight based on an age-weight curve, which was constructed by measuring nestlings of known age daily for 17 d post hatch (sample size varied between 8 and 44 nestlings depending on age; Strickland unpubl.). Using this growth curve for known-age nestlings, we were able to assess whether nestlings were larger or smaller than normal for their age.

Every female that was weighed consistently throughout the pre-laying period initiated a nest (n = 20 females). Additionally, there were two mated pairs that we were unable to weigh consistently throughout the pre-laying period (as their nests were only found in the incubation period), but we were able to monitor their 'nest success' (defined as whether a pair of birds successfully fledged young [yes/no] based on whether there were nestlings present at the time of banding). Since the probability of nest predation was low during the first 1–2 weeks of the nestling period, we assumed that predation probability was similarly low during the late nestling period, and so the presence of 11 d-old nestlings likely indicated successful fledging. The nests of three pairs failed in the incubation period but were followed by successful re-nests; these pairs were included in the analyses examining the factors influencing weight gain but were excluded from models examining the influence of rate of weight gain and final weight on first egg date, clutch size, number of nestlings, nestling condition or nest success.

Statistical methods

To describe the rate of weight gain in females in the 15 d prior to laying, we fitted both linear and power functions to the observed data (pooled across all females) and assessed model fit using Akaike's information criterion likelihood values adjusted for small sample sizes (AICc; Burnham and Anderson 2002). Males showed no evidence of weight gain over time so we report only the linear function. We used general linear models to assess the relationship between the beginning of weight gain and first-egg date, and to investigate the relationship between the rate of weight gain and final weight. Since the rate of weight gain was not correlated with final weight ($R^2 = 0.04$, $F_{1,18} = 1.81$, p = 0.20), we included both of these variables in subsequent models. In addition to the rate of weight gain, we felt that final weight could be an informative measure of pre-laying condition, particularly given that it appeared to be largely independent of initial weight ($R^2 = 0.09$, $F_{1,18} = 2.93$, p = 0.10) and body size (tarsus length: $R^2 = -0.05$, $F_{1,18} = 0.01$, p = 0.91; wing chord length: $R^2 = 0.07$, $F_{1,18} = 2.46$, p = 0.13). The total amount of weight gained (final weight – initial weight) was not included in any analyses since it was not independent of the rate of weight gain ($R^2 = 0.41$, $F_{1,15} = 12.10$, p = 0.003).

To investigate the factors influencing the rate of weight gain and final weight of females, we constructed general linear models including percent conifers and female age as

explanatory variables. We assessed whether the addition of these variables additively and interactively improved model fit, and compared these to a null model including only the intercept, using AICc. Models with good support were considered those with $\Delta AICc \leq 2$ (Burnham and Anderson 2002).

The influence of rate of weight gain and final weight on first egg date, clutch size, number of nestlings and nestling condition were assessed using general linear models, and nest success (binary variable) was assessed using a generalized linear model with a logit link function. An assessment of the generalized linear model supported the underlying assumption that the dispersion parameter was 1. A visual assessment of quantile-quantile and fitted versus predicted plots of residuals revealed no deviations from the underlying assumptions of normality and homoscedasticity in the general linear models. All analyses were conducted in R ver. 2.12.0.

Results

Patterns of weight change

The temporal change in the weight of females was best modeled with a power function ($f(x) = cx^b$; AICc = –628.23, $\Delta AICc = 0.00$, Akaike weight (w) = 1), suggesting that females increased their weight by a constant scaling factor (exponent 'b') during the pre-laying period (log-log, $\beta = 0.08 \pm 0.003$, $t_{192} = 22.8$, p < 0.0001; Fig. 1a). Females with higher rates of weight gain (steeper weight-gain curve) had a higher scaling factor. On average, females began gaining weight 9 d ($\pm$ 1) prior to first egg (mean first egg date: 18 March $\pm$ 7 d) and increased their body weight by 25 $\pm$ 6%. The difference in average female weight 15 d and 1 d prior to first egg was highly significant (paired t-test: $t_{19} = 20.91$, p < 0.0001; Fig. 1b) and there was no evidence that male weight changed over the same time period ($t_{37} = -0.20$, p = 0.83; Fig. 1b). Mean female weight 15 d before first egg date (67 $\pm$ 3 g; mean $\pm$ SD) was significantly lower than mean male weight at the same time (74 $\pm$ 4 g; $t_{37} = 6.34$, p < 0.0001; Fig. 1b) but female weight one day prior to first egg date (84 $\pm$ 3 g) was significantly higher than mean male weight at the same time (74 $\pm$ 4 g; $t_{36} = 8.39$, p < 0.0001; Fig. 1b).

Causes of weight gain

The rate of weight gain in females was best explained by the null model, although the second-ranked model, which included variation in female age as an explanatory variable, also received support (Table 1). Although the model result suggested that there was no effect of percent conifers on the rate of weight gain, visual inspection of the graph suggested that older females (> 3 yr) tended to have a higher rate of weight gain than younger females ($\leq$ 3 yr) and that young females on low percent conifer territories tended to have lower rates of weight gain than young females on high percent conifer territories (Fig. 2a).

Final weight in females was best explained by the variation in percent conifers on territories and female age, supporting both the carry-over effect and caching

experience hypotheses (Table 1). Final weight tended to be positively related to female age ($\beta = 0.58 \pm 0.18$, $t_{15} = 3.23$, p = 0.006; Fig. 2b) and was higher in females occupying territories with a higher percentage of conifers ($\beta = 0.12 \pm 0.05$, $t_{15} = 2.28$, p = 0.04). However, when females were split into two age categories ($\leq$ 3 [n = 7] and > 3 yr [n = 13]; Fig. 2b), this trend was only apparent in the older age category, likely due to the small sample size for females in the younger age category.

Consequences of weight gain

Females with higher final weights tended to produce larger clutches ($\beta = 0.24 \pm 0.08$, $t_{11} = 2.28$, p = 0.02; Fig. 3a) and there was weak evidence that they also hatched more nestlings ($\beta = 0.24 \pm 0.12$, $t_{10} = 2.00$, p = 0.07; Fig. 3b). Females with higher final weights also tended to have nestlings in better condition but the slope was not significantly different than zero ($\beta = 0.14 \pm 0.01$, $t_{13} = 1.56$, p = 0.14; Fig. 3c). Final weight did not influence first egg date ($\beta = -0.45 \pm 0.99$, $t_{12} = -0.45$, p = 0.66) or nest success ($\beta = 0.49 \pm 0.33$, z = 1.50, p = 0.13). There was no evidence that the rate of weight gain influenced first egg date ($\beta = -62.46 \pm 113.94$, $t_{15} = -0.55$, p = 0.59), but there was weak evidence that older females that exhibited higher rates of weight gain laid eggs earlier in the season ($\beta = -249.43 \pm 129.32$ $t_{11} = -1.93$, p = 0.08). We also found no evidence that the rate of weight gain influenced clutch size ($\beta = -12.69 \pm 15.94$, $t_{12} = -0.80$, p = 0.44), number of nestlings ($\beta = 2.81 \pm 21.59$, $t_{11} = 0.13$, p = 0.90), nestling condition ($\beta = -1.83 \pm 2.05$, $t_{13} = -0.90$, p = 0.39) or nest success ($\beta = -29.17 \pm 44.12$, z = -0.66, p = 0.51).

Discussion

Despite the predominantly foodless conditions prevailing during the gray jay's late winter pre-laying period, our results demonstrate that females were able to increase their weight dramatically before laying and even surpassed males several days before their first egg was laid. It is highly unlikely that this weight gain could be solely ascribed to the presence of the first egg in the oviduct because an egg is generally produced over 26 h and weighs approximately 10% of the females' body weight at the time it is laid (Perrins 1996, Gill 2007, Strickland and Ouellet 2011), and our final weight measurements likely took place > 20 h preceding the first egg. Prior to laying eggs, female gray jays increased their initial body weight by an average of 25 $\pm$ 6 % (mean $\pm$ SD), which is on par with non-caching species such as the blue tit *Parus caeruleus* (31.4%, Perrins 1996) but even higher than the wood duck *Aix sponsa* (14%, Drobney 1982), European sparrowhawk *Accipiter nisus* (15%, Newton et al. 1983) and pied flycatcher *Ficedula hypoleuca* (18.4%, Ojanen 1983). Thus, this finding is quite remarkable, particularly given that female gray jays are primarily consuming perishable food that was stored four or more months previously (Strickland and Ouellet 2011). Although females are assisted through supplementary feedings (also drawn from food stores) by their mates during the late pre-laying period (Strickland unpubl.), to our knowledge, this is the first evidence of
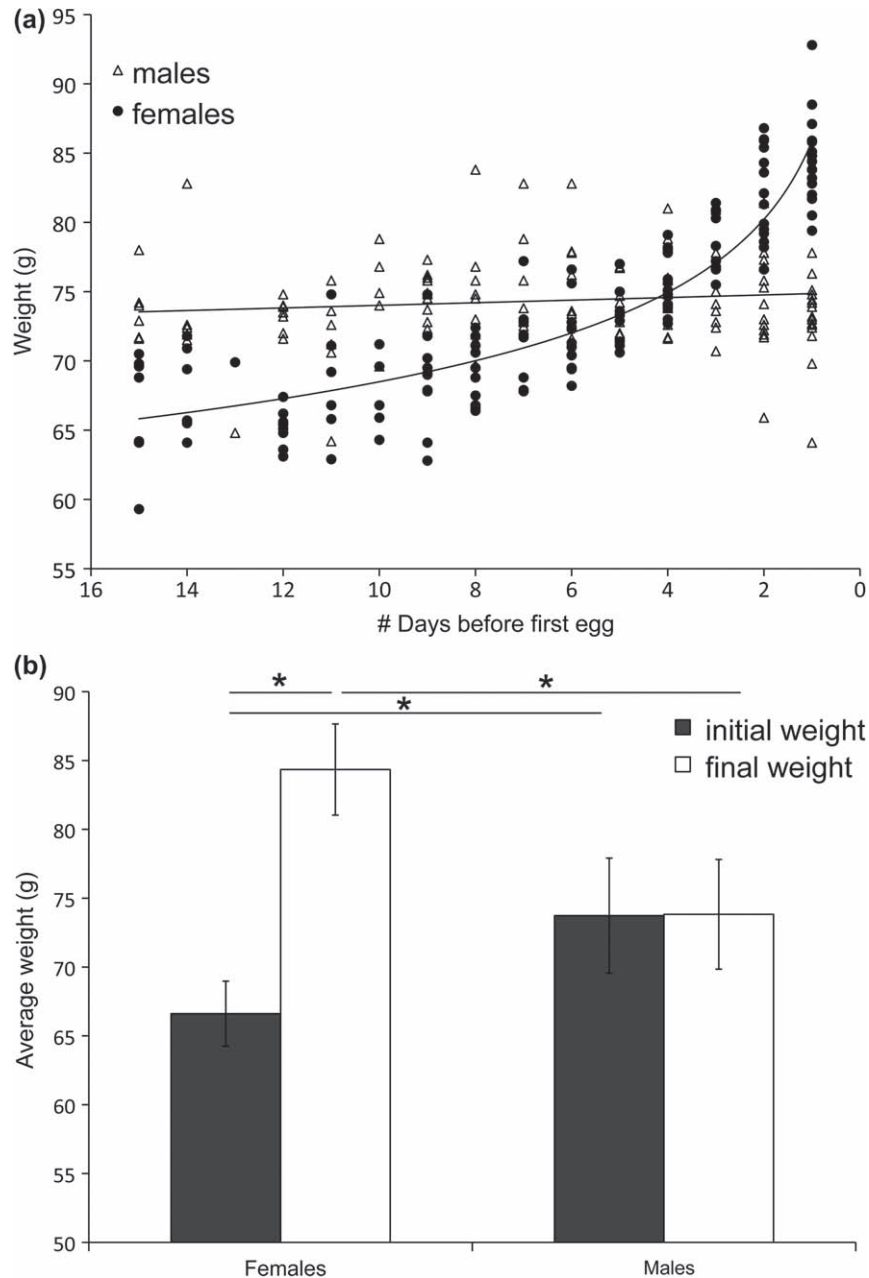
Figure 1. (a) Patterns of weight gain of females (n = 20) and males (n = 20) over the course of the pre-laying period (15 d prior to first egg). Female weight gain was best modeled with a power function (f(x) = cx^b); male weight was best modeled with a linear function (f(x) = cx + b); (b) mean weights of females and males 15 d prior to first egg date and 1 d prior to first egg date. Error bars represent standard deviations; asterisks represent significant differences (p ≤ 0.05) based on t-tests for differences between means.

female birds being able to gain weight prior to laying eggs by relying largely on cached food.

Our study also provides indirect evidence for a novel mechanism by which habitat quality could carry-over to influence female condition the following season. Habitat quality has been associated with higher fitness in numerous bird species (Nettleship 1972, Ens et al. 1992, Franklin et al. 2000), but specific mechanisms by which habitat quality influences female condition, such as the one presented here, are not often elucidated. Although the structural complexity of coniferous forests may potentially play a role in increasing the availability of cached food by better concealing caches

from competitors, previous work has provided experimental evidence that conifers are also better able to preserve cached food over a 2–4 month period (Strickland et al. 2011). Consistent with this, we show that the percentage of conifers on territories influenced the final pre-laying weight of females and, although not supported by model selection, the rate of weight gain showed a similar pattern, suggesting that the quality or quantity of food cached the previous fall carried over to influence pre-laying condition during the late winter. Although variation in habitat quality during the non-breeding season has been shown to influence breeding success in migratory (Norris et al. 2004, Saino

89

Table 1. Results of model selection for explaining the rate of weight gain during the 15 d before first egg (rate of weight gain) and final weight of females on the day prior to first egg (final weight) with respect to female age and the percent of conifers on territories (percent conifers). Within each response variable, models are ranked (best-worst) based on the change in AICc units (ΔAICc) and Akaike weights (w).

Response	Model	ΔAICc	w
Rate of weight gain			
	intercept	0.00	0.563
	female age	0.52	0.434
	percent conifers	12.30	0.001
	female age + percent conifers	12.79	0.001
	female age × percent conifers	13.06	0.001
Final weight	percent conifers + female age	0.00	0.837
	percent conifers × female age	3.92	0.118
	percent conifers	6.12	0.039
	female age	10.56	0.004
	intercept	12.98	0.001

Figure 2. Influence of territory quality (percent conifers on territory) and female age on (a) the rate of pre-laying weight gain ('rate of weight gain') and (b) weight on the day prior to first egg ('final weight') in female gray jays. Boxplots show medians (horizontal lines), 25th and 75th quartiles (upper and lower edges of boxes, respectively). Error bars represent maximum and minimum observations for each age class in each territory class.

et al. 2004, Sorensen et al. 2009) and non-caching, resident species (Cook et al. 2004, Descamps et al. 2008, Robb et al. 2008), there are fewer examples for caching species. Inman et al. (2012) reported that rock structure of caching sites influenced the preservation of kills by wolverines *Gulo gulo*. These habitat-mediated carry-over effects are likely important drivers of fitness in caching species given that the quality and quantity of food consumed during the winter is largely determined by factors such as food abundance and decay rates during the season prior to when food is actually consumed. In one sense, species that rely on stored food to breed can be thought of as a type of capital breeder (Drent and Daan 1980, Houston et al. 2006), where nutrient reserves are 'formed' outside the body several months prior to breeding, and used by females to attain breeding condition and form eggs.

Species that rely on perishable stored food for breeding may also be particularly susceptible to long-term changes in climate because of the extended period during which food is exposed to the environment. For example, warm temperatures during the fall and early winter may accelerate cache decay, which may in turn reduce food availability during the winter and this could carry over to influence reproductive success (Waite and Strickland 2006, Inman et al. 2012). Thus, for food-caching species, it is important to understand how earlier stages in the annual cycle can be linked to later stages, as this likely plays an important role in mediating variation in fitness and population dynamics.

Although both the rate of weight gain and final weight tended to increase with habitat quality, our results reveal that the final weight of females influenced clutch size and number of nestlings while the rate of weight gain did not. As such, the ability of female gray jays to attain a high final weight appears to be more important for maximizing reproductive output than the rate at which the weight is gained. This contrasts with findings from non-caching birds, which suggest that a prolonged period of pre-laying weight gain is linked to higher final weight and increased reproductive performance (Drent and Daan 1980, Newton et al. 1983). The difference between these studies and our findings could be due to the fact female gray jays may not need to build up body reserves prior to laying eggs in the same way that
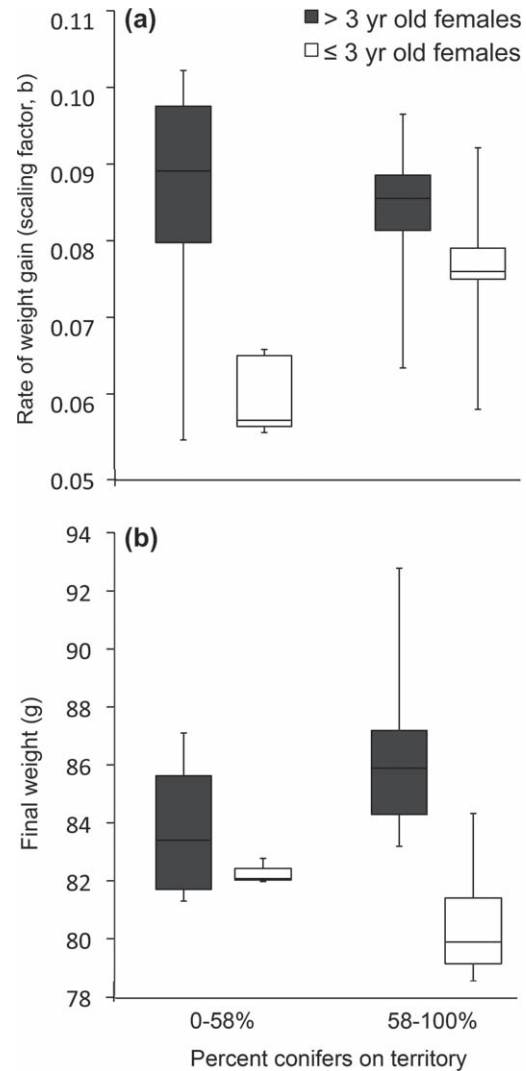
non-caching, 'capital breeders' do, since they can access stored food and increase their weight at any point during the pre-laying period. Non-caching capital breeders on the other hand tend to gradually accumulate internal stores in order to achieve a high body weight prior to laying (Drent and Daan 1980), likely because there is not enough food available to accumulate reserves more quickly, or because they may simply be constrained by searching and handling time (Martin 1987). In contrast, gray jays presumably remember the locations of all or much of their cached food and it takes little or no time to process caches once they are retrieved. Thus, it is perhaps not surprising that gray jays begin to deviate from their baseline weight only ~9 d before their first egg, while weight gain in non-caching species can begin 3–4 weeks prior to first egg (Newton and Marquiss 1984, Hohman 1986, Perrins 1996).
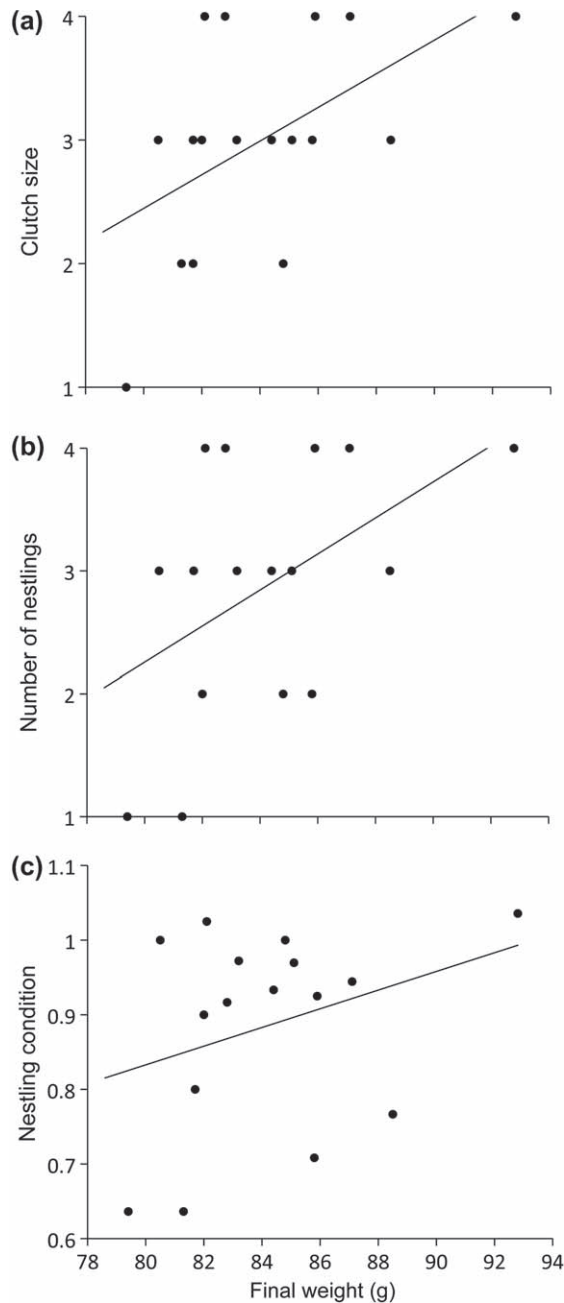
Figure 3. Relationship between female weight on the day prior to first egg date ('final weight') and (a) clutch size, (b) number of nestlings, and (c) observed/expected nestling age ('nestling condition'). Lines represent linear best fit.

Although we found that the final weight of females was a good predictor of variation in several reproductive performance indicators, it did not appear to influence the timing of breeding, suggesting that breeding decisions are made well before final weights are achieved. Indeed, the primary proximate factor that influenced first egg date was the date on which females began to increase their weight ($R^2 = 0.96$, $\beta = 0.98 \pm 0.05$, $t_{14} = 18.4$, $p < 0.001$). Thus, females appeared to be committed to begin breeding at a specific time when they initiated weight gain, which was 8–11 d before the first egg was laid. We are currently examining whether food abundance drives individual variation in the timing of weight gain.

In gray jays (Bunch and Tomback 1986) and other food-hoarding corvids (Kamil and Balda 1985, Clayton 1998), caching requires a highly developed spatial memory in order to successfully retrieve thousands of food items that are stored throughout territories, a process that is refined over a learning period early in life (Shettleworth 1990). We found that age positively influenced the final weight of females and that age showed a similar pattern with respect to rate of weight gain, which supports the hypothesis that older females are better able to store and/or retrieve cached food. An alternative to the caching experience hypothesis, however, is that older females are simply more familiar with their territories than younger females are, having spent more years occupying them (Loman 1984), which may lead to increased feeding efficiency for reasons unrelated to caching experience per se. Further, older females may be better at detecting cues that indicate optimal conditions for initiating nesting, due to increased breeding experience (Nol and Smith 1987), which could improve their ability to gain weight efficiently.

Interestingly, our results also show that the effect of conifers on final weight appeared to be stronger in older females (> 3 yr), compared to younger females (≤ 3 yr; Fig. 2b). It is possible that older females may be better able to exploit the increased food-storing capacity of high quality territories to attain a high final weight, whereas younger females are limited by experience. In this population, previous evidence has shown that reproductive output is lower in first-year breeders compared to older females (Waite and Strickland 2006). Our results provide a possible mechanism for this relationship: younger females may not be able to attain as high a final body weight as older females prior to laying eggs, especially in territories with a lower percentage of conifers, due to their inexperience with caching food, which in turn affects reproductive performance.

As a result of the relationship between habitat quality, female weight gain and reproductive performance, human-induced habitat changes such as thinning and selective harvesting may have negative implications for the conservation of gray jays, especially if coniferous tree stands are targeted. Commercial harvesting of conifers could directly affect gray jay populations by reducing the availability of vital caching sites. Forestry practices have been associated with reduced territory occupancy in Siberian jays *Perisoreus infaustus*, a close relative of the gray jay, and have also been shown to affect the reproductive success in this species by increasing the visibility of nests to aerial predators (Eggers et al. 2005, Griesser et al. 2007, Griesser and Lagerberg 2012). However, although commercial forestry does occur within the boundaries of Algonquin Park, our study site lies in a protected area (Ontario Ministry of Natural Resources 2002), such that changes in commercial harvesting within Algonquin are unlikely to directly affect our study population. Further, recent increases in the amount of protected forest within Algonquin have clear positive implications for the conservation of gray jays in Algonquin in general, since they protect habitat outside our study area, within currently commercially harvested regions of Algonquin Park (Ontario Ministry of Natural Resources 2012).

Our results provide evidence of a unique relationship between habitat quality and female caching experience and their influence on breeding season dynamics. Weight gain in females has been shown to be a key factor in explaining reproductive output (Newton and Marquiss 1981, Perrins 1996, Schoech 1996) and our study points to a mechanism that may explain variation in weight gain among females while controlling for annual variation in climate and food abundance. This study system also provides an opportunity to investigate the influence of habitat-mediated carry-over effects on female weight gain in the subsequent breeding season, a phenomenon that has rarely been observed in bird populations and merits further study.

References

Ankney, C. D. and MacInnes, C. D. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. – Auk 95: 459–471.

Arcese, P. and Smith, J. N. M. 1988. Effects of population density and supplemental food on reproduction in song sparrows. – J. Anim. Ecol. 57: 119–136.

Bunch, K. G. and Tomback, D. F. 1986. Bolus recovery by gray jays: an experimental analysis. – Anim. Behav. 34: 754–762.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. – Springer.

Clayton, N. S. 1998. Memory and the hippocampus in food-storing birds: a comparative approach. – Neuropharmacology 37: 441–452.

Cook, J. G., Johnson, B. K., Cook, R. C., Riggs, R. A., Delcurto, T., Bryant, L. D. and Irwin, L. K. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. – Wildl Monogr. 155: 1–61.

Dally, J. M., Emery, N. J. and Clayton, N. S. 2006. Food-caching western scrub-jays keep track of who was watching when. – Science 312: 1662–1665.

Descamps, S., Boutin, S., Berteaux, D., McAdam, A. G. and Gaillard, J. -M. 2008. Cohort effects in red squirrels: the influence of density, food abundance and temperature on future survival and reproductive success. – J. Anim. Ecol. 77: 305–314.

Dow, D. D. 1965. The role of saliva in food storage by the gray jay. – Auk 82: 139–154.

Drent, R. H. and Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. – Ardea 68: 225–252.

Drobney, R. D. 1982. Body weight and composition changes and adaptations for breeding in wood ducks. – Condor 84: 300–305.

Eggers, S., Griesser, M., Andersson, T. and Ekman, J. 2005. Nest predation and habitat change interact to influence Siberian jay numbers. – Oikos 111: 150–158.

Ens, B. J., Kersten, M., Brenninkmeijer, A. and Hulscher, J. B. 1992. Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). – J. Anim. Ecol. 61: 703–715.

Fletcher, Q. E., Landry-Cuerrier, M., Boutin, S., McAdam, A. G., Speakman, J. R. and Humphries, M. M. 2013. Reproductive timing and reliance on hoarded capital resources by lactating red squirrels. – Oecologia doi: 10.1007/s00442-013-2699-3.

Franklin, A. B., Anderson, D. R., Gutiérrez, R. J. and Burnham, K. P. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. – Ecol. Monogr. 70: 539–590.

Gill, F. B. 2007. Ornithology, 3rd ed. – W. H. Freeman.

Gosler, A. G., Greenwood, J. J. D. and Perrins, C. 1995. Predation risk and the cost of being fat. – Nature 377: 621–623.

Griesser, M. and Lagerberg, S. 2012. Long-term effects of forest management on territory occupancy and breeding success of an open-nesting boreal bird species, the Siberian jay. – For. Ecol. Manage. 271: 58–64.

Griesser, M., Nystrand, M., Eggers, S. and Ekman, J. 2007. Impact of forestry practices on fitness correlates and population productivity in an open-nesting bird species. – Conserv. Biol. 21: 767–774.

Hohman, W. L. 1986. Changes in body weight and body composition of breeding ring-necked ducks (*Aythya collaris*). – Auk 103: 181–188.

Houston, D. C., Donnan, D. and Jones, P. J. 1995. The source of the nutrients required for egg production in zebra finches *Poephila guttata*. – J. Zool. 235: 469–483.

Houston, A. I., Stephens, P. A., Boyd, I. L., Harding, K. C. and McNamara, J. M. 2006. Capital or income breeding? A theoretical model of female reproductive strategies. – Behav. Ecol. 18: 241–250.

Inman, R. M., Magoun, A. J., Persson, J. and Mattisson, J. 2012. The wolverine's niche: linking reproductive chronology, caching, competition and climate. – J. Mammal. 93: 634–644.

Kamil, A. C. and Balda, R. P. 1985. Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). – J. Exp. Psychol. Anim. B 11: 95–111.

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. – Ecology 67: 377–385.

Loman, J. 1984. Breeding success in relation to parent size and experience in a population of the hooded crow. – Ornis Scand. 15: 183–187.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. – Annu. Rev. Ecol. Syst. 18: 453–487.

McNamara, J. M., Houston, A. I. and Krebs, J. R. 1990. Why hoard? The economics of food storing in tits, *Parus* spp. – Behav. Ecol. 1: 12–23.

Nettleship, D.N. 1972. Breeding success of the common puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. – Ecol. Monogr. 42: 239–268.

Newton, I. and Marquiss, M. 1981. Effect of additional food on laying dates and clutch sizes of sparrowhawks. – Ornis Scand. 12: 224–229.

Newton, I. and Marquiss, M. 1984. Seasonal trends in the breeding performance of sparrowhawks. – J. Anim. Ecol. 53: 809–829.

Newton, I., Marquiss, M. and Village, A. 1983. Weights, breeding and survival in European sparrowhawks. – Auk 100: 344–254.

Nol, E. and Smith, J. N. M. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. – J. Anim. Ecol. 56: 301–313.

Norris, D. R., Marra, P. P., Montgomerie, R., Kyser, T. K. and Ratcliffe, L. M. 2004. Reproductive effort, molting latitude and feather color in a migratory songbird. – Science 306: 2249–2250.

Ojanen, M. 1983. Egg development and the related nutrient reserve depletion in the pied flycatcher, *Ficedula hypoleuca*. – Ann. Bot. Fenn. 20: 293–300.

Ontario Ministry of Natural Resources 2002. Algonquin Provincial Park Management Plan. – Queen's Printer for Ontario, Toronto, Canada.

Ontario Ministry of Natural Resources 2012. Algonquin Provincial Park – Proposed Management Plan Amendment. – <www.algonquinpark.on.ca/pdf/lighteningthefootprint_2012_amendment.pdf>.

Perrins, C. M. 1996. Eggs, egg formation and the timing of breeding. – Ibis 138: 2–15.

Persson, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. – Can. J. Zool. 83: 1453–1459.

Pravosudov, V. V. and Grubb, T. C. Jr 1997. Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. – Behav. Ecol. 8: 332–339.

Pravosudov, V. V. and Lucas, J. R. 2001. A dynamic model of short-term energy management in small food-caching and non-caching birds. – Behav. Ecol. 12: 207–218.

Robb, G. N., McDonald, A., Chamberlain, D. E., Reynolds, S. J., Harrison, T. J. E. and Bearhop, S. 2008. Winter feeding of birds increases productivity in the subsequent breeding season. – Biol. Lett. 4: 220–223.

Rutter, R. J. 1969. A contribution to the biology of the gray jay (*Perisoreus canadensis*). – Can. Field Nat. 83: 300–316.

Saino, N., Szép, T., Ambrosini, R., Romano, M. and Møller, A. P. 2004. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. – Proc. R. Soc. B 271: 681–686.

Schoech, S. J. 1996. The effect of supplemental food on body condition and the timing of reproduction in a cooperative breeder, the Florida scrub-jay. – Condor 98: 234–244.

Sherry, D. F. 1985. Food storage by birds and mammals. – In: Rosenblatt, J. S. (ed.), Advances in the study of behaviour. Academic Press, pp. 153–183.

Shettleworth, S. J. 1990. Spatial memory in food-storing birds. – Phil. Trans. R. Soc. B 329: 143–151.

Siikamäki, P. 1998. Limitation of reproductive success by food availability and breeding time in pied flycatchers. – Ecology 79: 1789–1796.

Smith, C. C. and Reichman, O. J. 1984. The evolution of food caching by birds and mammals. – Annu. Rev. Ecol. Syst. 15: 329–351.

Sorensen, M. C., Hipfner, J. M., Kyser, T. K. and Norris, D. R. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. – J. Anim. Ecol. 78: 460–467.

Strickland, D. 1991. Juvenile dispersal in gray jays: dominant brood member expels siblings from natal territory. – Can. J. Zool. 69: 2935–2945.

Strickland, D. and Waite, T. A. 2001. Does initial suppression of allofeeding in small jays help to conceal their nests? – Can. J. Zool. 79: 2128–2146.

Strickland, D. and Ouellet, H. 2011. Gray jay (*Perisoreus canadensis*). – In: Poole, A. (ed.), The birds of North America online. Cornell Lab of Ornithology, Retrieved from the Birds of North America Online: <http://bna/birds.cornell.edu/ban/species/040doi:10.2173/bna/40>.

Strickland, D., Kielstra, B. and Norris, D. R. 2011. Experimental evidence for a novel mechanism driving variation in habitat quality in a food-caching bird. – Oecologia 167: 943–950.

Vander Wall, S. B. 1990. Food hoarding in animals. – Univ. of Chicago Press.

Waite, T. A. and Strickland, D. 1997. Cooperative breeding in gray jays: philopatric offspring provision juvenile siblings. – Condor 99: 523–525.

Waite, T. A. and Strickland, D. 2006. Climate change and the demographic demise of a hoarding bird living on the edge. – Proc. R. Soc. B 273: 2809–2813.

Woodburn, R. J. W. and Perrins, C. M. 1997. Weight change and the body reserves of female blue tits, *Parus caeruleus*, during the breeding season. – J. Zool. 243: 798–802.