Seasonal variation in the effect of cache pilferage on cache and body mass regulation in Carolina chickadees: what are the trade-offs?

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Current dynamic optimization models predict that animals should respond to cache pilferage by decreasing the probability of caching food and by increasing internal fat storage to compensate for a reduction in cache size. We tested these predictions under laboratory conditions with variable food access (four 15-min intervals/day). Carolina chickadees (Poecile carolinensis) were subjected to two environments: under pilferage conditions, one-quarter of their cached seeds were stolen every 0.5 h, and under no-pilferage conditions, seeds were left in place. Half the birds started with pilferage conditions and were then switched to the no-pilferage condition; the other half started with no pilferage and were then switched to pilferage conditions. The experiment was conducted over the course of a year to test for seasonal variation in the response to seed pilferage. The birds responded to seed pilferage by taking more seeds from a feeder, suggesting that they monitored cache availability. Alternatively, the birds may have taken additional seeds from the feeder in response to increased hunger caused by a loss of cached food. Contrary to our prediction, birds cached a higher percentage of seeds from the feeder when cached seeds were pilfered than when caches were left in place. Treatment order also affected caching behavior for all but the summer birds: chickadees initially subjected to pilferage stored a higher proportion of seeds than those initially subjected to no pilferage. Caching percentages in the summer were unaffected by cache pilferage. Caching rates (number cached/day) also followed the same trends: rates were higher when seeds were pilfered than when seeds were not pilfered, and there was a treatment-order effect for all but the summer birds. Variation in body mass also failed to match predicted trends. All birds exhibited a monotonic increase in mass as the experiments proceeded, irrespective of treatment order. Controlling for this monotonic increase in mass, an analysis of residual variation in body mass indicated that birds gained less weight when seeds were pilfered than when seeds were left in place. Finally, birds tested in the fall and spring were heavier than those tested in the summer. These results fail to support the relationship between cache maintenance and body mass regulation predicted by current models of energy regulation. We discuss the applicability of three hypotheses for the observed trends. Key words: body mass, cache behavior, cache pilferage, chickadees, energy regulation, fat regulation, food storing, foraging behavior, hoarding behavior, Poecile carolinensis, seasonal variation, tits.

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cached instead of eaten, and therefore the index can be used to evaluate the decision to eat or cache a food item. Caching rate is a composite of the rate at which seeds are encountered and the proportion of these seeds that are cached; thus, the use of caching rate addresses the net result of both the bird's caching decisions and local environmental conditions.

The predictions assume that birds can monitor pilferage rates and adjust their caching behavior accordingly. We tested this assumption by comparing the number of seeds the birds took from a feeder when their caches were pilfered with the number taken when their caches were not pilfered. If the birds were monitoring the size of their caches, they should have taken additional seeds (which should be eaten) when their cache was pilfered. Finally, we addressed the potential for seasonal variation in the response to cache pilferage by conducting the experiment over the course of 1 year. Seasonal variation in body mass and cache regulation has been demonstrated in this group of birds (e.g., Lucas, 1994; Lucas and Walter, 1991; Ludescher, 1980; Shettleworth et al., 1995); therefore, it is reasonable to test for seasonal variation in chickadees' simultaneous regulation of body mass and cached food in response to cache pilferage.

METHODS

Chickadees were captured in sunflower seed-baited traps at Purdue University's Ross Biological Station, in West Lafayette, Indiana, USA. We used birds only if their wing chord length indicated that they were males (62–66 mm; Thirukput, 1985). We used only large birds to reduce potential individual variation caused by size (e.g., Lucas, 1994). All birds were held in 1-m³ holding cages for 1 week before being housed singly in 3 × 3 × 2-m experimental aviaries. Each aviary contained two electronic balances that recorded the bird's weight whenever a bird perched long enough for the balance to stabilize. The aviaries also contained 6 plastic trees with 10 cache sites in each tree. Virtually all seeds cached in the aviary were cached in the trees. An infrared sensor in each cache site was used to record cache and retrieval times (the birds stored only one seed in a cache site), from which cache durations could be calculated. Seeds were pilfered remotely using a solenoid attached to a trap door on the bottom of each cache site.

We tested six unique sets of three birds (18 individuals total) over the course of a year; the experimental design is listed below. The sets were started in October, December (1995), February, April, June, and August (1996). The dates can be broken into three categories based on seasonal changes in behavior (see Smith, 1991): fall/winter (October and December), when birds in the field are flocking; spring (February and April), when the flock breaks down (Smith, 1991, records a correlated increased rate of aggression in late February and March) and mating occurs; and summer (June and August) when the territory jointly held by the male and female breaks down, and the fall flocks begin to reform.

The light/dark cycle was 10/14 h and aviary temperature was 19±1°C throughout the experiment. To the extent that external conditions influence nutrient requirements (e.g., through their effect on activity budgets and metabolic rates), these constant conditions were used to standardize conditions under which the birds were run at various times during the year. Our previous results (Lucas, 1994; Lucas and Walter, 1991) showed that chickadees show season-appropriate responses even under these constant short-day conditions.

The aviaries were cleaned at 1700 h every night. This involved moving each bird into a small holding cage attached to its aviary. After 30–45 min of cleaning and restocking of feeders, the birds were returned to the aviaries. Seeds cached in the trees were left in place overnight. We removed any seeds that were not cached in the trees (this amounted to fewer than five seeds for each bird over the course of the experiment).

Birds in holding cages (before the experiment began) received two mealworms (about 0.4 g) daily and sunflower seeds, grated carrot, and "soft-bill" bird food ad libitum. Two sources of food were available in the experimental aviaries. Every night at 1730 h, the birds received 0.25 g of mealworms, 0.5 g grated carrot (which they rarely ate), 0.25 g "soft-bill" bird food, and crushed egg shell. This food remained in the aviaries until the following evening, although the mealworms were always eaten immediately. The second source of food was shelled sunflower seeds, delivered from an electronic feeder.

We trained the birds to use the feeder over the course of 4 days, after which the experimental regime was started. For the first day of training, seeds were delivered from the feeder ad libitum. The second day, access to the feeder was limited to 100 min, divided among 16 equal-length intervals randomly distributed throughout the day (0800–1700 h). For the final 2 days of the training period, the birds were given the same feeder schedule they would experience during the experiment: a total of 60 min of access to food divided among four intervals randomly distributed throughout the day. No seeds were pilfered during the training period. This schedule of episodic food availability has been shown to promote high caching rates (Hurry, 1992; Lucas et al., 1993). In addition, previous aviary experiments (Lucas, 1994; Lucas and Walter, 1991) demonstrated that, under circumstances similar to those used here, chickadees are capable of regulating cache size and body mass at equilibrium levels when given only 40 min of access to food. Thus, the 60 min of access used here was more than sufficient to allow for regulation of both cache size and body mass.

We broke the experiment into one pilferage time block and one nonpilferage time block. Each block lasted 12–13 days. In the pilferage time block, all cache sites were censused remotely every half hour while the lights were on and each cached seed was pilfered with a probability of 0.25 (note that the computer-read infrared sensors are censused several times per second to monitor cache and retrieval times). No seeds were stolen at night. In the no-pilferage time block, all seeds were left in place. Nine (of 18 total) different birds (3 sets of 3) started the experiment with the pilferage treatment and were then switched to no pilferage. The other nine birds started with no pilferage and were then switched to pilferage. The experimental design is illustrated in the figures. For example, six sets of birds are represented in Figure 1; each set consists of three individuals. The first set, begun in October, was given the no-pilferage treatment first and was then shifted to the pilferage treatment. The second set, begun in December, started with the pilferage treatment and then switched to no pilferage.

The duration of time (12–13 days) the birds were given in each treatment block was set a priori. A previous experiment (Lucas and Zielinski, unpublished data) indicated that it takes at least 5 days for caching behavior and body mass to equilibrate under new experimental conditions. Thus, 12 days should have been sufficient time to generate a response to the pilferage treatment while permitting a reasonable sample size (18 birds total). We did not use the first 6 days of data in any given treatment in the analyses.

Statistical analysis

We used repeated-measures ANCOVA with a first-order autoregressive covariance structure (PROC MIXED; SAS Institute, 1994) to test our predictions. Three dependent variables were used in the models: dawn mass/wing-chord (see below), per-
generate interpolated body mass estimates. The order of determination was to reduce the amount of information required to used in the equation. The rationale for the regression equation (PROC GLM; SAS Institute, 1990) in order of increasing polynomial regression equation (PROC GLM; SAS Institute, 1990). A separate equation was generated for each day's data. Each value is the mean of three birds (all individuals were used in only one set); error bars are SDs. Data are given separately for pilferage and no-pilferage treatments; symbols are arranged chronologically within each set of birds. (—) No caches stolen; (P) one-quarter of caches stolen per 30 min. Closed circles represent birds first experiencing no pilferage; open circles represent birds first experiencing pilferage.

Mean number of seeds taken from the feeder per day for the six sets of Carolina chickadees tested. Each value is the mean of three birds (all individuals were used in only one set); error bars are SDs. Data are given separately for pilferage and no-pilferage treatments; symbols are arranged chronologically within each set of birds. (—) No caches stolen; (P) one-quarter of caches stolen per 30 min. Closed circles represent birds first experiencing no pilferage; open circles represent birds first experiencing pilferage.

percentage of seeds taken from the feeder during the day that were cached, and the number of seeds cached per day (i.e., cache rate). We used dawn mass because it represents the minimum body mass attained by birds and has been explicitly used as an index of body reserves in previous models (e.g., Lucas and Walter, 1991; also see Lucas, 1994). Mass was divided by wing chord length to help standardize for the size of the bird (as in Lucas, 1994). In the statistical models, we used an arcsine square-root transform of the percentage of seeds cached (Sokal and Rohlf, 1981). Q-q plots were used to test for normality in the residuals of the regression equations (see Khattree and Naik, 1995). Treatment order (i.e., whether the birds started with their seeds being pilfered or not pilfered) and season were treated as class variables in the PROC MIXED analyses. We used a dummy variable to evaluate the effect of pilferage rate: pilferage rate was arbitrarily treated as 1 for no-pilferage time blocks and 2 for pilferage time blocks. Nonlinear relationships between dependent and independent variables (listed below) were tested by adding squared terms of each independent variable. Two-way interaction terms between all independent variables were also added to the models, along with the three-way interaction treatment-order × pilfer-rate × season (see below). Nonsignificant (p > .05) interactions and squared terms were dropped from the models in order of increasing F value.

We used an interpolation of the mass data recorded from the electronic balances to estimate dawn mass, which we operationally define as mass at 0800 h. We used an interpolation because we were not certain to measure a bird's weight at exactly 0800 h, despite having more than 100 weights throughout the day for each bird. Also, the birds often roosted off the perch balance, so we could not reliably use weight before lights-on. The interpolation used a fourth-order least-squares polynomial regression equation (PROC GLM; SAS Institute, 1990). A separate equation was generated for each day's data. Mass was estimated from two independent variables, time-of-day, and time since the feeder last opened (or since 0800 h if the feeder had not opened yet). All interaction terms through the square of the independent variables were also used in the equation. The rationale for the regression equation was to reduce the amount of information required to generate interpolated body mass estimates. The order of the regression equation (fourth) was the minimum required to generate an R² of .9 for all days.

We used mean values per bird to examine the relationship between the effect of pilferage on body mass regulation and the effect of pilferage on caching behavior, using treatment order and season as covariates in a simple least-squared-means regression model. For each bird we calculated (1) Δ(% cached) = (x % cached/day when seeds were pilfered) - (x % cached/day when seeds were not pilfered), (2) Δ(cach e rate) = (x number cached/day when seeds were pilfered) - (x number-cached/day when seeds were not pilfered), and (3) Δ(relative mass) = (x dawn mass/wing-chord when seeds were not pilfered) - (x dawn-mass/wing-chord when seeds were pilfered). We treated Δ(relative mass) as an independent variable in the regression models.

RESULTS

Caching During the course of the day, each bird took approximately 30–50 seeds from the feeder (Figure 1). The birds used an average of 93.1 (±7.6 SD in means for each bird) of the 60 cache sites (range 54–60) over the course of the experiment and had, on average, about 4 seeds already in the cache sites when they cached a seed (mean of means for each bird: 4.1 ± 2.4SD for pilfer environment, 4.5 ± 3.6SD for no-pilfer environment). These data indicate that cache sites were not limiting.

Cached seeds remained in the cache site an average of approximately 1 h before being retrieved (the time seeds were left in caches during "lights-out" was not included in these values), although the variance in cache duration was high and the distribution was right skewed (Figure 2; note that these data exclude pilfered seeds). Some recaching of seeds was evident; the birds occasionally retrieved and recached seeds after the feeder was closed. This recaching will cause our measure of cache duration to underestimate the total time that seeds were cached in the avairy. One way to evaluate whether this recaching caused seeds to be cached for long periods of time is to calculate the number of seeds left at dusk (i.e., at lights out). In fact, most birds left few seeds in the caches over night (Figure 3). Thus, even considering recaching of seeds, seeds were typically left in cache sites for less than a day.

We predicted that birds would be less likely to cache a seed when stored seeds were pilfered from their caches than when
seed were not pilfered. This prediction was wrong. The birds cached a higher proportion of seeds when cached seeds were pilfered compared to conditions where caches were untouched (Figure 4). However, the response to pilferage is complicated by two additional effects, treatment order and season. Compared to birds whose seeds were initially not stolen, birds initially exposed to pilferage cached a higher percentage of seeds overall and cached relatively more seeds when seeds were stolen. In addition, caching in response to pilferage did not increase in the summer. Summer birds also failed to exhibit a higher caching percentage for birds first experiencing pilferage. The combined effects of seed pilferage, treatment order, and season is reflected in a significant three-way interaction among these terms (Table 1). The number of days of experience did not account for a significant amount of variation in caching behavior (Table 1).

The same trends were seen with caching rates (seeds cached/day) as with percentage of seeds cached (Figure 5). Seeds were cached at greater rates during the pilferage treatment than during the no-pilferage treatment in all seasons but summer, when no trend was evident. The birds also cached at higher rates when their first experience in the aviary was the pilferage treatment compared with birds first given the no-pilferage treatment (note the significant pilfer rate × treatment order × season interaction in Table 2).

Compensation

If the birds were able to monitor the pilfering of their seeds, they should be able to compensate for this cache loss by taking additional seeds from the feeder (assuming that they do not stop caching). This was tested as follows: the dependent variable in our regression analysis was the mean number of seeds taken from the feeder when seeds were stolen minus the mean number of seeds taken when seeds were not stolen (this is the excess seeds taken during pilfering). The independent variable was the mean number of seeds pilfered from each bird per day.

Birds did indeed compensate for pilfered seeds by taking extra seeds from the feeder (Figure 6; effect of pilferage on excess taken: \( F_{1,17} = 9.4, p = .007 \). This relationship does not differ with treatment order (\( F_{1,19} = 1.0, p = .33; n.s. \). The regression equation for the relationship is: \( \Delta \) number seeds taken/day = \( -2.10 \pm 1.71 \) + \( 0.99 \pm 0.25 \) number of seeds pilfered/day. The slope suggests that, on average, one additional seed was taken for each seed stolen from the cache (intercept: \( t = -1.23, p = .24 \); slope: \( t = 4.02, p = .001 \);
Table 2
Repeated-measures regression analysis of seed caching rates (seeds cached per day; see Figure 5)

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>F (df)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pilfer rate</td>
<td>6.44 (1,12)</td>
<td>.026</td>
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<tr>
<td>Treatment order</td>
<td>4.54 (1,14)</td>
<td>.056</td>
</tr>
<tr>
<td>Season</td>
<td>2.87 (2,14)</td>
<td>.090</td>
</tr>
<tr>
<td>Pilfer rate X treatment order X season</td>
<td>3.74 (5,12)</td>
<td>.028</td>
</tr>
<tr>
<td>No. days of experience</td>
<td>5.17 (1,17)</td>
<td>.036</td>
</tr>
</tbody>
</table>

See Methods for a discussion of pilfer rate, treatment order, and season effects.

However, only 50% of the variance is accounted for the regression (i.e., $r^2 = .50$), so the compensation was not perfect.

Body mass

Our prediction was that the birds should compensate for pilferage by gaining weight. This prediction was wrong, and the assumption behind the prediction (a pilferage-induced decrease in caching rates) was also wrong. All birds gained weight through the experiment irrespective of whether their seeds were originally pilfered (Figure 7, Table 3).

Controlling for the time trend, pilferage rates, treatment order, and seasonal effects did account for a significant amount of variation in body mass (Table 3). Birds were lighter when seeds were pilfered than when they were not pilfered (correlation coefficient = $-0.0034 \pm 0.0015$; $t_{14} = -2.3$, $p = .028$). Also, birds whose seeds were stolen initially tended to be heavier than those whose seeds were not stolen initially (Figure 7, Table 3). Finally, birds tested in the fall and spring were heavier than those tested in the summer (fall versus summer: $t_{14} = 6.4$, $p = .0001$; spring versus summer: $t_{14} = 5.0$, $p = .0002$; Figure 7, Table 3).

We tested for correlated effects of pilferage on body mass regulation and on caching behavior using treatment order and season as covariates. Neither the change in percentage of seeds cached ($\Delta$ (% cached)) nor the change in caching rates ($\Delta$ (cache rate)) was significantly related to mass change ($\Delta$ (relative mass); Figure 8; change in percent cached: $F_{1,14} = 2.1$, $p = .17$; change in caching rates: $F_{1,14} = 8.6$, $p = .003$).

The change in caching behavior was significantly affected by treatment-order (Figure 8: change in percent cached: $F_{1,14} = 4.7$, $p = .048$; change in caching rates: $F_{1,14} = 9.7$, $p = .008$), and by season (Figure 8: change in percent cached: $F_{1,14} = 19.0$, $p = .0007$; change in caching rates: $F_{1,14} = 18.8$, $p = .007$). Both of the latter results support the repeated-measures analyses discussed earlier (see "Caching").

The data illustrated in Figure 8 also show that the trends discussed above are robust. Focusing on the y-axis (caching behavior), all six birds started with the pilferage treatment in the fall and spring sets and all three birds started with the no-pilferage treatment in the fall cached a higher percentage of seeds in the pilferage treatment than in the no-pilferage treatment (Figure 8a). The same is true with caching rates (Figure 8b). Also, the increase in mass across all birds is indicated by the uniformly negative values for $\Delta$ (relative mass) for birds initially given the pilferage treatment and by the uniformly positive values for birds initially given the no-pilferage treatment.

DISCUSSION

Our original prediction was that birds should be less likely to store food and more likely to store fat when their seeds are pilfered (Lucas and Walter, 1991; McNamara et al., 1990; also see Hurly, 1992). The prediction assumes that the cost of car-

![Figure 7](https://example.com/Figure7.png)

Mean body mass/wing-chord of Carolina chickadees. Data are given separately for pilferage and no-pilferage treatments; symbols are arranged chronologically within each set of birds. (---) No caches stolen; (P) one-quarter of caches stolen per 30 min. Closed circles represent birds first experiencing no pilferage; open circles represent birds first experiencing pilferage.

![Figure 6](https://example.com/Figure6.png)

Effect of the mean number of seeds pilfered from a cache on the excess number of seeds taken by a bird from the feeder when seeds were pilfered (i.e., number taken per day in the pilferage time block = number taken per day in the no-pilferage time block). Each symbol represents a different bird. Solid line: regression line for all birds combined.

![Table 3](https://example.com/Table3.png)

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>F (df)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pilfer rate</td>
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<td>.034</td>
</tr>
<tr>
<td>Treatment order</td>
<td>5.94 (1,14)</td>
<td>.029</td>
</tr>
<tr>
<td>Season</td>
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<td>.0001</td>
</tr>
<tr>
<td>No. days of experience</td>
<td>37.8 (1,17)</td>
<td>.0001</td>
</tr>
</tbody>
</table>

See Methods for a discussion of pilfer rate, treatment order, and season effects.
risk and energy expenditure inherent in higher fat loads (see Smith (1990), for example, suggested that hoarding overcompensation is commonly stated in the literature. Kallander and Lima, 1986; Witter and Cuthill, 1993). Ekman and Hake, 1990; Lima, 1986). Controlling for the current literature. There is some debate about exactly how long caches last before being pilfered (Brodin, 1992, 1993; Lucas and Walter, 1991; McNamara et al., 1990; but see Hitchcock and Houston, 1994) and the seasonal variation in energy storage that is commonly exhibited by animals (Lucas, 1994; Lucas et al., 1993; Mrosovsky, 1990; Zielinski, 1996). However, we suspect that this change in scope would not alter the predictions unless some other structural changes were added to the models.

Three alternative hypotheses might be consistent with our results. First, our results could be an artifact of the conditions we used in the aviaries. For example, the pilferage rates may be artificially high or the pattern of food availability could be beyond the birds' ability to gauge. Unfortunately, the resolution of this issue is beyond the scope of this study and beyond the current literature. There is some debate about exactly how long caches last before being pilfered (Brodin, 1992, 1993; Sherry et al., 1982; Stevens and Krebs, 1986), and no such data have been published specifically for Carolina chickadees. Pilferage rate will certainly vary with location (e.g., Stapanian and Smith, 1986) and food-type cached (e.g., Stapanian and Smith, 1984). Moreover, details of the temporal pattern of food availability are simply unknown for most parids. It has proved difficult to gather these data, although Brodin’s (1992, 1993) use of radioactively labeled seeds offers a potentially useful technique for measuring seed retrieval rates. In addition, we do not have a sufficient number of laboratory studies to address the universality of our results. At this point, we assume that our results are a reflection of normal energy regulation patterns in chickadees.

Second, despite our assumptions to the contrary, cache levels may be regulated independently of fat loads (also see Pravosudov and Grubb, 1997). The cache itself may be important, and the response to a threat to cached food may simply be to increase the effort required to maintain the cache. As a simple example, assume that a bird required 10 cached seeds at the end of the day. The bird might increase its caching rate to offset any threat to the cache caused by potential pilferage and thereby increase the chance that at least 10 seeds are left at dusk. The effect of treatment order in our experiment supports this conclusion: when we pilfered seeds as soon as the experiment started, birds cached more than when no seeds were pilfered for the first 12-15 days of the experiment. Thus, when chickadees “knew” only that the aviary was not safe for cached food, they cached at relatively high rates to compensate for the pilferage.

The birds’ response to pilferage suggests that cache dynamics do not strongly influence body mass regulation. To some extent, this would be expected if the time scale of cache regulation was distinct from that of mass regulation (Lucas and

![Figure 8](https://academic.oup.com/beheco/article-abstract/9/2/193/215516/193)

(A) Change in mean percentage of seeds cached as a function of change in mean relative mass. (B) Change in caching rate (seeds cached/day) as a function of change in relative mass. In all cases, “change” is the mean during the pilferage treatment minus the mean during the no-pilferage treatment. Each symbol represents a different bird. Solid symbols: birds initially given no-pilferage treatment; open symbols: birds initially given pilferage treatment.

An analysis of residual variation in body mass indicated that birds gained significantly less weight when seeds were pilfered than when seeds were left in place, contrary to the prediction.

Compensation for pilferage did occur. The number of extra seeds taken from the feeder in the pilferage time block correlated with the average number of seeds pilfered from each bird. Thus, at least one aspect of foraging behavior increased when seeds were pilfered, but body mass did not. We did not test for other potential forms of compensation. For example, Hampton and Sherry (1992; also see Kamil et al., 1993) showed that black-capped chickadees (Poecile atricapillus) could learn to avoid caching in areas of an aviary where seeds were stolen. However, no evidence was found for avoidance of randomly pilfered sites (Baker and Anderson, 1995), the pattern of pilferage used in our experiment.

Why are our experimental results so at odds with the logic of energy regulation found in the literature? It could be that our models need to be expanded in scope to include both the short-term effects typically considered in models of energy regulation (e.g., Grubb and Pravosudov, 1994; Hurly, 1992; Lucas and Walter, 1991; McNamara et al., 1990; but see Hitchcock and Houston, 1994) and the seasonal variation in energy storage that is commonly exhibited by animals (Lucas, 1994; Lucas et al., 1993; Mrosovsky, 1990; Zielinski, 1996). However, we suspect that this change in scope would not alter the predictions unless some other structural changes were added to the models.

Our experimental results argue against this view of energy regulation. Instead, birds responded to seed pilferage by caching more, and no simple increase in body mass compensated for the pilfered seeds. The birds showed a monotonic increase in mass over the course of the experiment irrespective of pilferage treatment. This increase in mass may be a response to the variable food-access schedule the birds were placed on (e.g., Ekman and Hake, 1990; Lima, 1986). Controlling for this monotonic increase in mass, an analysis of residual variation in body mass indicated that birds gained significantly less weight when seeds were pilfered than when seeds were left in place, contrary to the prediction.
Walter, 1991). For example, tits occupying northern latitudes cache seeds in fall that they retrieve over the course of months (Vander Wall, 1990), yet seasonal variation in body mass is often less than daily variation in body mass (e.g., Haftorn, 1989). In species of this type, we should expect cache and body mass regulation to be relatively uncoupled (Lucas and Walter, 1991). In contrast, while both body mass regulation and caching rates have long-term components in Carolina chickadees and similar species occupying more southern latitudes (Lucas, 1994; Lucas et al., 1995), a majority of variation in both behaviors is shown over time scales on the order of days (Haftorn, 1989; Hurly, 1992; but see Brodin 1993, 1994). Theoretically, these circumstances should cause coupling of these alternative forms of energy storage (Lucas and Walter, 1991).

The similar time scales (i.e., within day) over which body mass and cached food were regulated by our birds under laboratory conditions (see Brodin, 1993, 1994) should have caused the regulation of these energy sources to be coupled. Indeed, one part of this relationship is well established: under many conditions, both birds and mammals cache more when body mass falls below regulated levels (Fantino and Cabanac, 1980; 1986; Lucas and Walter, 1991; Lucas et al., 1995; Zielinski, 1996; but see Lucas, 1994 and Pravosudov and Grubb, 1997). This correlation is consistent with the expected coupling in body mass and cache size inherent in the predictions we tested. This underscores the fact that a reduction in caching behavior is expected at relatively higher pilferage rates for a number of reasons—yet no trend was found. Thus, while variation in body mass affects the regulation of the cache, variation in cache size does not strongly influence body mass regulation.

Third, contrary to our assumptions, cache levels may not be regulated as state variables. By treating cache size as a state variable, models of cache maintenance implicitly assume that feedback exists between the rewards derived from cached food and subsequent caching behavior (e.g., Hurly, 1992; Lucas and Walter, 1991; McNamara et al., 1990). This feedback is also assumed to be fundamentally the same as the feedback between rewards derived from fat and subsequent eating behavior. However, some intriguing indirect evidence indicates that cache regulation may not include these types of feedback. Caching rates in rats are linearly related to body mass, with an x-intercept at the body mass set point (i.e., the equilibrium body mass that rats appeared to "defend"; Fantino and Cabanac, 1980). In chickadees and titmice, the probability that food is cached is linearly related to body mass (Lucas, 1994; Lucas and Walter, 1991; Lucas et al., 1993). This relationship was used to show how body mass set-point changes with ovarian cycles (Fantino and Brinnel, 1986) and with changes in temperature (Fantino and Cabanac, 1984). In the rat experiments, cache size was measured by simply removing the cache. This design was used to ensure that caching rates were independent of body mass regulation and therefore that caching rates were an open-looped index of body mass regulation and set-point (see Fantino and Cabanac, 1980). However, this design implicitly assumes no effect of cache pilferage on further caching behavior. Similar results were collected on marsh tits (Mason and Clayton, in preparation); birds continued to cache irrespective of whether the caches were completely pilfered.

Many rodents increase caching rates in the fall when faced with an overabundance of food sources (i.e. the flush of seeds that develops in the fall). Nyby and Thiessen (1980) hypothesized that this behavior could be driven by increasing body mass set-points at that time of year. Thus, rodents faced with excess food may nonetheless be hungry if their regulated level of body mass increases more rapidly than their actual mass levels. This hunger would in turn promote high levels of caching. Here again, the lack of feedback between cache dynamics and cache behavior is implicit in the hypothesis.

Our results show that chickadees compensate for stolen caches by taking additional food from the feeder; this seems to contradict the third alternative hypothesis, a lack of feedback in the caching cycle. Nonetheless, it is possible that the birds are simply more likely to cache food when the interval between feedings increases (as it would when caches are stolen); mild deprivation levels enhance caching tendencies in a number of species (Vander Wall, 1990; see Lucas et al., 1995, for a demonstration of this in Paridae). Thus, the compensation we measured could be a direct result of changes in the diurnal pattern of deprivation levels.

It could be said that this third hypothesis addresses proximate levels of behavioral regulation and that ultimate regulation of caching behavior is still adequately addressed assuming that cache size can be treated as a state variable. However, treating cache size as a state variable requires some level of feedback between the dynamics of the cache and future caching decisions. If this feedback does not exist, then the structure of the models has to be altered.

Chickadees responded to seed pilferage by increasing the proportion of seeds cached in all seasons except summer. Body mass regulation also showed a seasonal component; birds in summer were lighter than birds tested in other seasons. This seasonal variation appears to be part of a much broader seasonal pattern in energy regulation. Many species increase caching rates (Vander Wall, 1990) and body mass (Dark and Zucker, 1985; Heldmaier, 1989) in the fall compared to other times of year. A number of more subtle seasonal changes have also been found. Under laboratory conditions, chickadees show a seasonal shift in diet, preferring seeds in winter and insects in summer (Lucas and Walter, 1991; see also Godler, 1987). We previously showed that chickadees in the fall and winter increase caching rates when subjected to reduced food access, but under the identical conditions in late spring and summer, the birds stopped caching (Lucas, 1994; see Shettleworth et al., 1995). Similarly, hummingbirds (Hiebert, 1991) and starlings (Witter et al., 1995) increase mass in response to food restriction in the spring (or under short-day conditions) and decrease mass in response to food restriction in the summer (or under long-day conditions).

These seasonal trends have two possible components: one is a change in the level of storage of fat and cached food that is likely to reflect a change in the trade-offs associated with the storage of these energy forms (Witter et al., 1995). A reduction in fat load and cache size in the summer should reflect a decrease in the benefit accrued from energy storage when food levels are high. A second component to these trends is the degree to which either fat or cached food levels are defended (Mrosovsky, 1990). The data reported here suggest that chickadees fail to alter caching behavior in the summer in the face of a threat to their cache. Our previous results showed that chickadees faced with reduced access to food in the summer reduced caching rates, even though this caused them to lose weight rapidly (Lucas, 1994). While there are examples of an adaptive reduction in regulated levels of fat stores, most notably in birds caring for young (Moreno, 1989; Mrosovsky and Sherry, 1988), the results of our studies of chickadees suggest that the behavioral and physiological defense of energy storage levels also has a cost and that these birds do not pay that cost in the summer months. It would be interesting to know whether these seasonal trends in energy regulation are coincident with seasonal changes in spatial memory (Clayton and Cristol, 1996) and hippocampal structure (Barnea and Notebohm, 1994; Smulders et al. 1995).
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