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Management of fat reserves in tufted titmice (*Parus bicolor*): evidence against a trade-off with food hoards

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Abstract Caching species can manage their energy supply by adjusting body fat, number of caches, or both. It has been hypothesized that because body fat has a higher fitness cost than caches, small food-hoarding birds respond to increased starvation risk by increasing the number of their caches rather than their fat load. This hypothesis predicts that when birds cannot cache they should compensate for the loss of external energy storage by (1) shifting the time of their daily body mass accumulation toward earlier in the day and (2) increasing the overall level of their fat reserves. During the winter of 1995–1996, we tested these predictions with a caching species, the tufted titmouse (*Parus bicolor*). Each of six experimental birds was fed a diet of uncachable sunflower seed powder for 6 days, preceded and followed by 6-day control periods during which they were fed cachable sunflower seeds. The daily pattern of body mass gain was unaffected by the opportunity to cache. Furthermore, when unable to cache, the birds did not increase either their mean daily body mass, body mass in the middle of the day, or evening body mass compared to the two control periods. These results argue against the hypothesis of a trade-off between fat reserves and food caches in tufted titmice, and suggest that fat reserves are managed independently of external food caches.

Key words Fattening · Food-caching · Trade-off · Energy management · Starvation risk

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Introduction

In high latitudes, wintering diurnally active homeotherms are adapted to survive low ambient temperatures, long nights, and reduced levels of food. To decrease the probability of starving, wintering birds adjust the level of their energy reserves (Lima 1986; McNamara et al. 1990, 1994; Witter and Cuthill 1993; Grubb and Pravosudov 1994). While birds that do not cache food can adjust only their fat reserves, birds that make external food caches appear to have more complex options for energy management.

It has been shown that birds carry more fat during the winter (e.g., King 1972; Haftorn 1989), and several experimental studies have demonstrated that when birds perceive an increased risk of starvation, they increase their fat reserves (Ekman and Hake 1990; Hake 1996; Witter et al. 1995). However, since fat reserves are never increased to their maximal limit (King 1972; Blem 1990), body mass changes have been modeled as a trade-off between the risk of starvation and the risk of predation (Lima 1986; McNamara and Houston. 1990). Hypothesized costs of increased fat include increased maintenance metabolism and increased diurnal predation risk due to either reduced maneuverability (Witter et al. 1994) or reduced vigilance (Lima 1986; McNamara and Houston 1990).

Since food caches represent an alternative energy source for some wintering passerines, McNamara et al. (1990) hypothesized that there could be a trade-off between fat reserves and food caches. While non-caching birds should gain fat reserves steadily throughout the day, food-caching birds could delay gaining fat while storing energy as food caches instead. Late in the day, then, caching birds could rapidly consume their food caches to build up fat reserves for the subsequent nocturnal fasting period (Fig. 1).

McNamara et al. (1990) also proposed that as starvation risk increased, food-caching birds could increasingly substitute food caches for fat reserves. In a

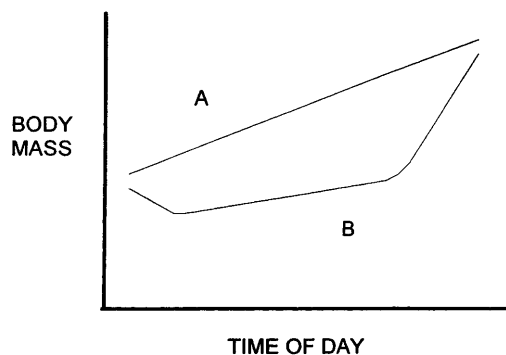


Fig. 1 Daily routine of body mass variation in **A** non-caching and **B** caching birds expected from the McNamara et al. (1990) model

previous study (Pravosudov and Grubb 1997), we demonstrated that tufted titmice (*Parus bicolor*) increased both food caches and fat reserves in response to unpredictable food supply, suggesting that the two forms of energy may be largely independent. However, because the titmice were always able to cache food in that study, the results did not test whether there was a trade-off between food caches and fat reserves. Here, we evaluate the trade-off hypothesis directly by monitoring body mass of titmice unable to cache food.

We tested two predictions derived from the McNamara et al. (1990) trade-off hypothesis. First, if there is a trade-off between food caches and fat reserves, normally food-caching birds should change their daily routine of fat accumulation when they are prevented from caching. In particular, if deprived of caches, such birds should resemble non-caching species by shifting mass gain towards the morning (Fig. 1). Second, if deprived of caches, birds that normally cache food should increase their body mass to compensate for loss of the alternative energy source.

Methods

Six male tufted titmice (sexed by wing length, T.C. Grubb, unpublished work) were caught at different locations in central Ohio and tested individually in an outdoor aviary 3 m × 8 m × 2 m high. The aviary was open to the sky (except for wire netting), but was walled by translucent white fiberglass panels that isolated a bird visually and eliminated wind in the aviary. One end of the aviary was roofed by a translucent white fiberglass panel 30 cm wide that protected a “recording” perch and feeder from rain and snow. The aviary contained five caching “trees” fashioned from sugar maple (*Acer saccharum*) saplings, each bearing 20 evenly-distributed holes 0.5 cm in diameter and 1 cm deep for the birds to use as cache sites. An observation chamber was located at one end of the aviary, separated from it by a wall of one-way glass.

The experiments were conducted under prevailing photoperiods; outdoor ambient temperatures were stored in a computer every 30 min (Weather Wizard III and Weatherlink software; Davis Instruments). An electronic balance (Mettler, Toledo) inside the observation chamber was connected through the one-way glass wall to a perch in the aviary. As this perch was the highest available in the aviary, birds used it frequently during the day and always

roosted on it at night. Readings from the balance were recorded to the nearest 0.01 g and stored in a computer to provide a continual record of body mass. The system checked the balance every second and stored records of body mass and time of day whenever a bird was sitting on the perch. At night, the system recorded body mass and time every minute.

Procedure

We tested the six titmice individually between the end of November 1995 and the beginning of April 1996. We followed an 18-day protocol consisting of three 6-day phases: pre-treatment, treatment and post-treatment. Before being tested, a bird spent about a week in a cloth-covered 1-m³ holding cage followed by 4–5 days in the aviary with food *ad libitum*.

When on *ad libitum* food, titmice in our system made few if any caches (Pravosudov and Grubb 1997). Therefore, to induce the birds to cache when they could, we endeavored to increase the birds’ perceived starvation risk during all three phases of the experiment. In nature, food availability and predictability appear to vary simultaneously and, presumably, birds respond to both changes at the same time (Pravosudov and Grubb 1997). Therefore, in our experiment, we altered both availability and temporal predictability of food, and assumed that birds responded to the combination of these two variables as influencing their risk of starvation. We divided a day into four 2-hour time blocks from 0900 to 1700 hours. Access to food was limited to one randomly chosen 30-min period of the four possible 30-min periods within each 2-h block. During that 30-min period, food was provided *ad libitum*.

During the two control periods of the experiment, the birds were provided with shelled sunflower seeds which they cached in the aviary. During the experimental period, the birds were provided only with sunflower seed powder, a food identical to the seeds in composition, but not cachable. Such powdered food did not appear to have any deleterious effect on the titmice and has been shown not to cause any significant mass changes and/or health problems in other tit species, even when supplied for relatively long periods of time (Clayton 1994, 1995). Thus, over the course of the experiment, all birds were maintained on unpredictable food that they could cache during the pre- and post-treatment periods, but not during the intervening treatment period.

Data collection and analysis

Body mass was recorded continually and daytime records were averaged to provide mean body mass for each 30-min time interval. We employed four measures to test the predicted effects of treatment on a bird’s body mass: (1) mean rate of mass gain, calculated as the mean of the four 30-min mass gains during each of the first and last two hours of the day and (2) evening body mass, defined as a bird’s body mass at the time it settled down to roost for the night on the recording perch, (3) mean daily body mass, calculated as the mean of the 30-min averages of a bird’s body mass during daytime, and (4) midday body mass, measured at the time midway between a bird’s first leaving the roosting perch in the morning and returning to the roosting perch for the night.

During each of the four 30-min time blocks when food was available, we observed each bird visually and recorded the number of caches it made.

We investigated changes in dependent variables within each bird and across the six birds. Before reducing records of body mass to mean values for the across-bird analysis, we checked for any within-bird effects of ambient temperature using ANCOVAs with treatment as a factor and ambient temperature as a covariate for each bird independently.

To compare responses using the bird as the primary sampling unit, we employed mean values of each dependent variable. For all dependent variables we compared control and treatment means using Wilcoxon matched-pairs signed ranks tests.

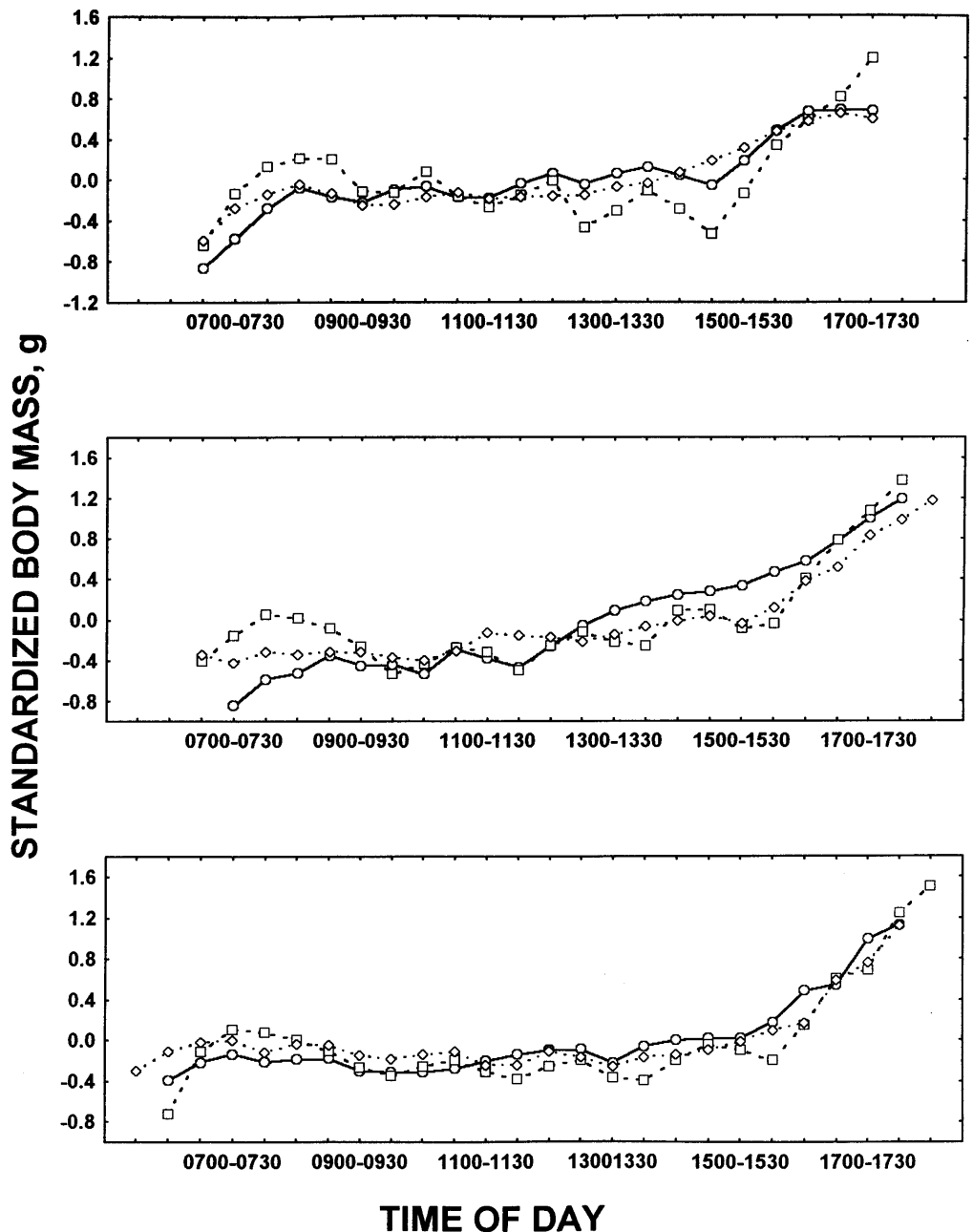
Results

Temperature was not significantly associated with any of the dependent variables within birds. The six titmice cached an average of 7.9 ± 3.8 (SD) and 18.7 ± 2.6 (SD) seeds per day, respectively, during the first and second control periods. No caches were made during the treatment period when birds had access only to powdered seeds.

Counter to the first prediction, when unable to cache, the birds did not shift their mass gain towards morning (Fig. 2). Mean body mass gain rates during the first 2 h and the last 2 h of the day were no different between the treatment and combined control periods (morning,

$z = 0.314, P = 0.753$; evening, $z = 0.943, P = 0.345$). Furthermore, mean body mass gain was significantly lower in the morning than in the evening in all three experimental periods ($z > 1.99, P < 0.04$). To evaluate the trajectories of body mass within a day independent of mean daily body mass, we transformed each control and treatment curve to deviations about a daily mean of zero (see Hurly 1992). For each of the six birds, the patterns of all three mass curves were nearly identical (Fig. 2), indicating that the ability to cache had no effect on the daily routine of body mass. The mean value of transformed body mass for the entire daily trajectory was even slightly lower for the treatment period compared to either pre-treatment, post-treatment or the combined pre- and post-treatment periods ($z < 1.2$,

Fig. 2 Transformed daily routine of body mass in six individual tufted titmice. Values in each of the three curves are in relation to a transformed mean value of 0 g for the entire curve (Hurly 1992). Circles represent pre-treatment, squares treatment, and diamonds post-treatment means



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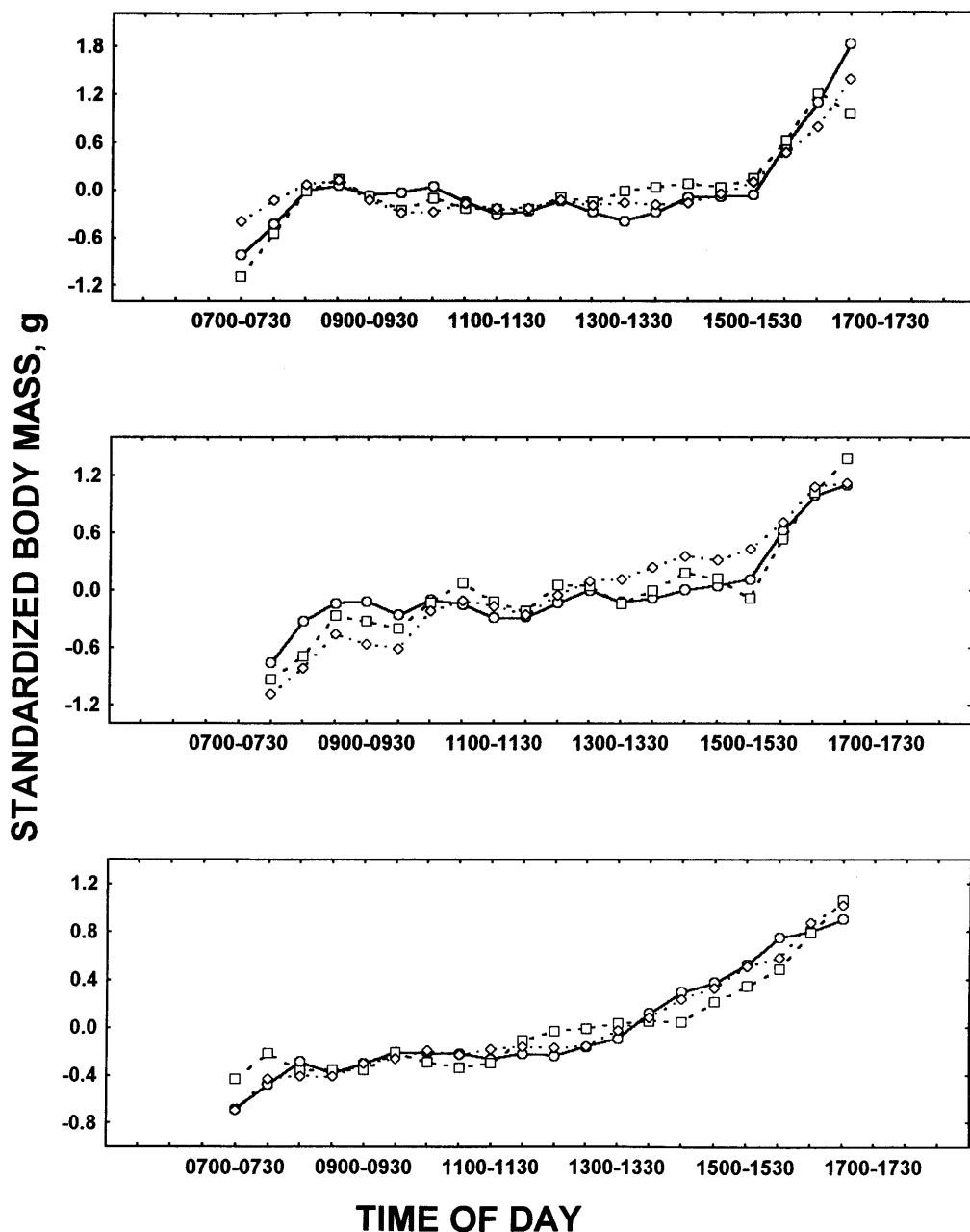


Fig. 2 (Continued)

$P > 0.12$), demonstrating no significant differences among the daily mass trajectories.

All birds significantly increased their evening body mass when they were moved from an *ad libitum* to an unpredictable food schedule at the beginning of the experiment ($z = 2.201$, $P = 0.028$). Because food was kept unpredictable throughout each 18-day replicate, we expected the birds to gradually increase their mass across all three phases of the experiment, as had subjects in several previous studies (Ekman and Hake 1990; Pravosudov and Grubb 1997). In fact, the titmice did increase their evening body mass between first control and treatment ($z = 1.78$, $P = 0.07$), and also between treatment and second control period ($z = 1.99$, $P = 0.04$).

Such results indicate that there was a lasting effect of switching to unpredictable food at the beginning of the first control period.

To control analytically for such a long-term effect and to discover whether our treatment had any further impact on evening body mass, we fit a single regression line for evening body mass across all three phases of the experiment and calculated residuals about the line. Such a method is routinely employed when two control periods are statistically different from each other and/or when some consistent trend is expected across control and treatment groups (e.g., Bednekoff et al. 1994). The prediction tested held that when prevented from caching, the titmice should carry more fat than when they are able to

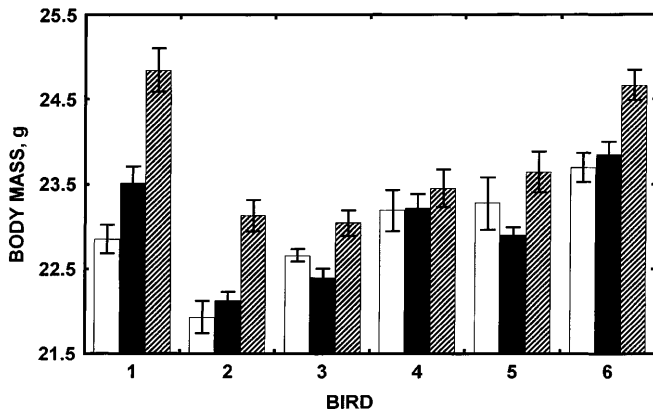


Fig. 3 Midday body mass of six tufted titmice. The *panels* of the figure are arranged from *left to right* in the order the birds were tested over the course of one winter. The first (*open*) and last (*shaded*) bars are associated with means for the 6-day control periods when cacheable food was available in the form of shelled sunflower seeds. During the intermediate 6-day period (*solid bars*), birds were furnished only with sunflower seed powder, a food type they were not able to cache. Vertical lines denote standard errors

cache. Thus, if there were a trade-off between food caches and body fat, mean residuals from the common regression of evening body mass should be greater for the treatment period than for the control periods. The residuals from pre- and post-treatment periods were nearly identical ($z = 0.733$, $P = 0.46$). Furthermore, the difference between evening body mass residuals for the treatment period and the combined control periods was non-significant ($z = 0.524$, $P = 0.60$).

Also contrary to the trade-off hypothesis, there was no significant difference in midday body mass between treatment and pre-treatment periods ($z = 0.31$, $P = 0.75$, Fig. 3), while midday body mass was significantly higher during the post-treatment than during the treatment period ($z = 2.20$, $P = 0.028$, Fig. 3). Mean daily body mass was also not significantly different between pre-treatment and treatment ($z = 0.54$, $P = 0.54$) and it, also, was higher during the post-treatment than during the treatment ($z = 2.20$, $P = 0.028$, Fig. 4).

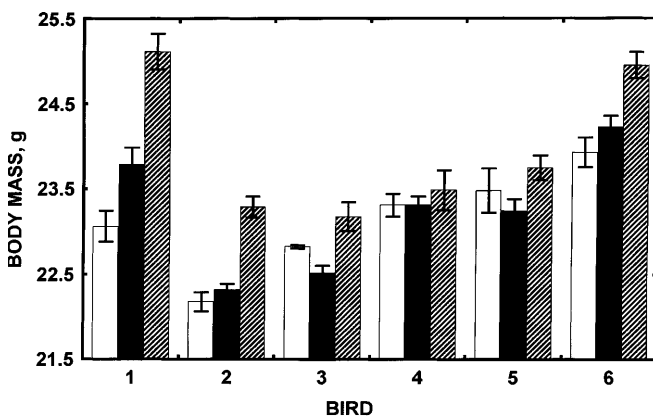


Fig. 4 Mean daily body mass of six tufted titmice. All notation as in Fig. 3

Discussion

Before interpreting our main findings, we consider why the birds' evening body mass and caching rate were consistently higher during the second than the first control period. When experimental birds are exposed to unpredictable food, they continually increase their body mass over a number of days before stabilizing at a new, higher level (Ekman and Hake 1990; Hake 1996; Pravosudov and Grubb 1997). Apparently, in the present experiment, the birds did not reach a stable adjustment of their evening fat supply within 18 days after their food supply had been made unpredictable. However, midday and mean daily body mass stabilized during the treatment period, increasing again only during the post-treatment period.

All birds cached significantly more seeds per day, on average, during the post-treatment than during the pre-treatment control period. The difference was due primarily to very intensive caching during the 1-st day of the post-treatment control, during which the six titmice cached a mean of 73.8 ± 17.6 (SD) seeds. By contrast, the daily mean for the last 4 days of the post-treatment was 7.1 ± 4.3 (SD) caches, a number very close to the mean caching rate of 7.9 seeds per day during the pre-treatment period. Perhaps the birds' caching on the first day of the post-treatment control was a strong reaction to having been unable to cache during the previous 6 days. The birds may then have returned to their normal pre-treatment rate of caching after having again built up some adequate number of caches.

Contrary to the predictions deduced from the McNamara et al. (1990) trade-off hypothesis, when unable to cache food, the titmice neither changed their daily routine of fat accumulation nor increased their evening body mass. McNamara et al. (1990) hypothesized a striking difference in tactics of daily routine of mass accumulation between caching and non-caching bird species based on a trade-off between food caches and body fat. In contrast to their hypothesis, our results showed that titmice did not alter their daily routine of fat accumulation when they could not cache and were forced to rely on fat as their only energy reserve. If birds were gaining mass faster over the course of a day during the treatment period, as predicted by the McNamara et al. (1990) model, then the mean value of daily body mass or transformed daily body mass should have been higher during that period. We found no statistical differences in mean transformed daily body mass among all three periods, a strong indication that the daily routine of mass gain was not affected by the inability to cache. Lack of any difference among the three treatments in body mass gain during either the first or the last 2 h of the day provides additional support for similarity of daily mass trajectories. Even though rapid accumulation of fat reserves early in the day should serve as a reliable tactic to achieve a safe level of fat reserves to survive the night, some counter pressure, most probably the risk of

predation, causes birds to delay intensive mass gain until later in the day whether they have caches or not.

While the analysis of evening body mass residuals demonstrated that there was no difference between treatment and controls in fat supply at roosting time, the model of McNamara et al. (1990) predicted the biggest difference in body mass during the day. The analyses of midday body mass and mean daily body mass showed that there was no significant difference between pre-treatment and treatment, and that the birds were actually heavier during the post-treatment than during the treatment period. These results argue strongly against the hypothesis of a trade-off between food caches and fat reserves.

Certainly, the value of our study is somewhat limited because we tested only six birds and because our treatments lasted only 6 days. However, the fact that birds did not increase their midday and mean daily body mass during the treatment and increased both during the post-treatment indicates that the birds had enough time to make some adjustments in body mass.

It appears that the titmice were managing their fat reserves as an energy resource independent of food caches. Such a conclusion has indirect support from other studies which showed that both caching and non-caching birds increased body mass when their food supply became unpredictable. For example, in both the food-caching willow tit (*Parus montanus*) and the non-caching greenfinch (*Carduelis chloris*), social subordinates carried more fat than dominant conspecifics (Ekman and Lilliendahl 1994; Hake 1996). Furthermore, it was shown that subordinates dropped their mass when the dominants were removed and that dominants increased their mass when energetic demands were made higher. Both studies concluded that while dominants might have a predictable food supply, allowing them to carry a smaller amount of body fat, subordinates always have a more unpredictable food supply since they can always be supplanted from a food item by the dominants, and as a result, subordinates must maintain a higher level of fat reserves. The similarity of fattening responses in the two studies supports our conclusion that fattening serves as the primary mechanism for reducing the risk of starvation in both caching and non-caching birds. Food caches then serve as a secondary mechanism increasing predictability of the food supply.

Available data suggest that birds that normally cache food with insufficient levels of fat reserves either do not cache food at all or cache less compared with birds with relatively high fat levels (Lucas and Walter 1991; Lucas 1994; Pravosudov and Grubb 1997). Perhaps, when food is unpredictable and starvation risk is high, an animal with insufficient fat reserves should first gain fat, rather than make caches, to meet imminent energetic requirements. When a sufficient level of fat reserves is achieved, an animal's starvation risk in the immediate future is reduced to the point where it can invest time in caching to provide predictable food for the less immediate future (Lucas and Walter 1991; Lucas 1994). Thus, it seems possible that while fat reserves are not influenced by

presence or absence of external food caches, food caching is affected by the extent of fat reserves.

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