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A dynamic model of short-term energy management in small food-caching and non-caching birds

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The survival of small birds in winter is critically dependent on the birds' ability to accumulate and maintain safe levels of energy reserves. In some species, food caching facilitates energy regulation by providing an energy source complementary to body fat. We present a dynamic optimization model of short-term, diurnal energy management for both food-caching and non-caching birds in which only short-day, winter conditions are considered. We assumed that birds can either rest, forage and eat, forage and cache, or retrieve existing caches (the two latter options are available only to caching birds). The model predicted that when there is variability in foraging success (here modeled strictly as within-day variability), both caching and non-caching birds should increase their fat reserves almost linearly in the morning slowing down toward late afternoon, a result consistent with field data but different than the result of a previous dynamic program. Non-cachers were predicted to carry higher fat levels than cachers especially when the variability in foraging success is high. Probability of death for non-caching birds was predicted to be higher than that for cachers, especially at higher levels of variability in foraging success. Among caching birds, an increase in number of caches and fat reserves was also predicted if: (1) mean foraging success was decreased, (2) variability in foraging success was increased, and (3) energy expenditure at night was increased over our baseline conditions. Under the conditions simulated in our model, birds were predicted to cache only if cache half-life (i.e., time interval over which 50% of the caches are forgotten or lost to pilferage) exceeded 2.5 days, indicating that low pilferage rate and long memory favor more caching. Finally, we showed that such daily patterns of energy management do not necessarily require relaxing assumptions about mass-dependent predation risk. *Key words:* caching, dynamic model, foraging, predation risk, pilferage. *[Behav Ecol 12:207–218 (2001)]*

During the non-breeding season, many small birds are faced with harsh conditions of short days, unpredictable food, and low ambient temperature. Under such demanding conditions, an animal should gain enough energy both to meet maintenance costs and to withstand possible high variability in food supply and/or other ecological conditions that can limit access to food (e.g., Bednekoff and Houston, 1994a,b; Lucas and Walter, 1991; McNamara and Houston, 1990; Pravosudov and Grubb, 1997a,b).

Theoretical analyses have indicated that high fat loads may also increase the risk of predation either through a reduction in maneuverability or through an increase in foraging time caused by increased metabolic demands (Lima, 1986; McNamara and Houston, 1990). However, tests of predation risk tradeoffs associated with maneuverability have proved equivocal. For example, some experiments demonstrated that heavier birds have slower flight speed and lower ascent angle during take off compared to leaner conspecifics (Metcalfe and Ure, 1995; Witter et al., 1994), whereas other experiments failed to find a substantial effect of body mass on flight characteristics (Kullberg, 1998; Veasey et al., 1998).

The question of how much energy a bird should maintain and how it should accumulate energy during the day has attracted much attention (Bednekoff and Houston, 1994a,b; Grubb and Pravosudov, 1994; Haftorn, 1989, 1992; Pravosudov and Grubb, 1997a,b, 1998; Witter and Cuthill, 1993). In general, both theoretical and empirical results suggest that birds should increase their mass when food becomes less predictable, when nights become longer, and when ambient temperature declines (Bednekoff and Krebs, 1995; Bednekoff and Houston, 1994a,b; Ekman and Hake, 1990). Several models predict that passerine birds should continue mass gain throughout the day to reduce the risk of starvation during the day and to ensure that enough reserves are stored to survive the night, a trend supported by empirical evidence (Bednekoff and Houston, 1994b; Lehikoinen, 1987; McNamara et al., 1994; see also reviews by Pravosudov and Grubb, 1997a; Witter and Cuthill, 1993).

Most of the literature addressing the issue of energy reserves has considered birds that only store energy internally as body fat (e.g., Pravosudov and Grubb, 1997a; Witter and Cuthill, 1993). However, many animals store energy externally as caches in addition to their storage of fat (Vander Wall, 1990); the joint regulation of these two energy stores has important life-history consequences. Although many animals, including both birds and mammals, must manage their fat and cache supplies during the winter, the nature of tradeoffs of energy storage in birds, determined by flight requirements, appear to be very different from that of mammals (see review by Witter and Cuthill, 1993). The first dynamic model of energy management in a caching passerine was published by McNamara et al. (1990). The main conclusion from that model was that in contrast to the predictions listed above for non-caching birds, caching birds should lower their body mass during the first part of the day in order to keep the risk of predation low and then they should gain mass rapidly during the last part of the day. The prediction rests on the assumption that caches represent a highly predictable food supply which caching birds can draw on at the end of the day to build up necessary energy reserves and the assumption that carrying fat reserves involves costs. Unfortunately, there is scant evi-

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Table 1

Mean ± SD number of caches for morning, midday, and evening at four levels of variance in foraging success

Variance	Morning	Midday	Evening
0.0	0.07 ± 0.27	0.07 ± 0.27	0.07 ± 0.27
0.004	9.60 ± 1.34	9.94 ± 1.22	9.84 ± 1.31
0.01(baseline)	29.06 ± 2.80	30.05 ± 2.77	29.78 ± 2.83
0.02	45.10 ± 4.38	46.57 ± 4.56	46.22 ± 4.48

Foraging success is measured in g fat accumulated in 20 min.

Table 2

Mean daily mass gain (g) and daily probability of death in caching and non-caching birds at four levels of variance in foraging success

	Mass gain		Probability of death/ 24 h (×10^4)	
Variance	Caching birds	Non-caching birds	Caching birds	Non-caching birds
0.0	0.73	0.73	6.29	6.29
0.004	0.73	0.74	6.64	6.77
0.01 (baseline)	0.74	0.78	7.07	8.08
0.02	0.74	0.81	7.38	9.75

Foraging success is measured in g fat gained in 20 min if found food is eaten.

dence supporting the predicted daily routine of mass gain in food-storing birds and some existing data argue against it (Haftorn, 1989, 1992).

In another dynamic model of cache and fat regulation, Lucas and Walter (1991) did not specifically address daily patterns of energy regulation; instead they focused on expected trends across days. In addition, they simulated fixed periods of access to food that mimicked laboratory conditions (Lucas and Walter, 1991). It is not clear if these predictions apply to more natural patterns of access to food.

Brodin (2000) recently addressed the disparity between diurnal mass trajectories described from field observations and those predicted by McNamara et al. (1990). Brodin (2000) suggested that the only way to generate theoretically derived mass trajectories that are similar to those observed in the field was to manipulate the mass-dependent component of predation risk. Specifically, he suggested that a relaxation of the assumption of a strictly monotonic relationship between mass and predation risk would generate mass trajectories similar to those found in the field. However, this conclusion is inconsistent with the results of Lucas and Walter (1991) who showed that the relative shape of the predation-risk function should have little effect on energy regulation patterns (also see Lucas and Howard, 1995). Since the sole focus of the Brodin (2000) paper was factors regulating diurnal mass trajectories, we feel that it is prudent to revisit this conclusion.

We present a model that considers energy management of both caching and non-caching birds. Our model includes a number of assumptions that appear to be more realistic than those found in previous models. We ask whether our new assumptions lead to a better match between predictions and data. We also address the validity of conclusions drawn by Brodin (2000) based on a similar model. Finally, we investigated the effect on our predictions of changing a number of parameters that characterize winter conditions. The conditions we evaluated include food availability, variability in foraging success, nocturnal temperature, mortality rates, and parameters that define caching patterns of birds such as mean energetic gain from retrieval, variability in retrieval gain, and cache pilferage rate. This exercise will also provide general lessons on the factors that affect how organisms manage energy in harsh and unpredictable environments.

MODEL

We developed a stochastic, dynamic optimization model (Mangel and Clark, 1988) with two state variables: fat reserves and food-caches. The optimal state-dependent decision matrix was calculated assuming that the birds maximize over-winter survival, which depends on energy reserves and predation risk. Mean daily patterns of body mass, eating, caching and retrieving intensities, and probability of death were estimated from the optimal decision matrix using forward simulation (as in McNamara et al., 1990).

We modeled a small food-caching bird such as the Carolina chickadee, black-capped chickadee (*P. atricapillus*) or willow tit. We assumed that body mass may vary from 8.0 to 12.0 g (Lucas 1994; Lucas and Walter, 1991; Pravosudov VV, and Lucas JR, personal observation) and that variation in mass is caused by differences in fat stores (Blem, 1990). We divided the 4.0 g of fat reserves into 100 increments. Increasing the number of increments to 150 (retaining a range of 4.0 g of fat) had no effect on the results. We assumed a maximum cache size of 300 food items divided into 300 increments. The birds are assumed to scatterhoard food (Vander Wall, 1990), and therefore each cached item is stored independently of other cached items. Increasing the upper limit to 400 items had no effect on the results of the model. A linear interpolation was used to estimate survival consequences of fractional increments of both fat reserves and cache size.

We divided an active day of seven h (which approximately corresponds to December in, for example, Edmonton, Alberta, Canada [55° 42′ N] or Lund, Sweden [55° 33′ N], into 21 20-min time intervals. During each 20-min time interval, a bird could perform one of four alternative behaviors: forage and eat, forage and cache, retrieve existing caches, or rest. A non-caching bird could only forage and eat, or rest. We decreased the time interval to 10 min for several simulations and found no effect on the predictions, and therefore assumed that the results from 20-min intervals are robust. All real variables in the program were declared as double precision (see Houston et al., 1997). In all cases, both backward (i.e., the dynamic program) and forward simulations equilibrated before 65 days. We therefore used this length as a conservative duration for all simulations. We used a single set of parameters for our baseline model, and tested the effect on the predictions of altering a number of these parameters. Each component of the model is listed below, and baseline parameters are specified in each section (also see Tables 1–5).

Starvation risk

Following Lucas and Walter (1991), we assumed that above some critical mass (minimal body mass [8 g] plus 10% of the maximum body mass range [4 g] or 8.4 g) the risk of starvation was zero. We used an incomplete beta function to calculate the probability of starvation below that mass. Parameter values for the incomplete beta function were taken from Lucas and Walter (1991).

Predation risk

We modeled predation risk as a two-stage process, the probability of a predator attack and the probability of depredation if an attack occurred (as in Lima, 1986; Lucas and Walter,

Table 3

Effect of mean foraging success on mass, maximum cache size and daily probability of death

Mean foraging success (g fat/20 min)	Morning mass (g)	Evening mass (g)	Number of caches	Probability of death/ 24 h ($\times 10^4$)
0.14	8.65 ± 0.22	9.32 ± 0.29	11.19 ± 10.46	1887.04
0.17	8.83 ± 0.15	9.57 ± 0.15	92.95 ± 23.31	11.09
0.19 (baseline)	8.70 ± 0.08	9.44 ± 0.08	30.05 ± 2.69	7.07
0.22	8.67 ± 0.08	9.40 ± 0.08	16.26 ± 1.65	5.54
0.24	8.62 ± 0.08	9.35 ± 0.08	6.36 ± 1.50	4.55

1991). When a bird was resting, its probability of being killed by a predator was zero. When a bird was active, the attack probability per 20-min time interval ($\alpha = 6.67 \times 10^{-4}$, recalculated from Lima, 1986) was constant. If attacked, the bird's probability of capture (p_{capture}) was mass-dependent. Lima (1986) assumed an accelerating quadratic function, although the relationship he used is nearly linear over the range of mass we used in our model (Figure 1A). Current empirical data (Kullberg, 1998) suggest that linear relationship between mass and predation risk is highly unlikely. Therefore for our baseline model, we chose an arbitrary function with predation-risk values similar to Lima's (1986) at extreme mass levels ($p_{\text{capture}} = .078$ at mass = 8 g; $p_{\text{capture}} = .173$ at mass = 12 g), but also included accelerating risk with an increase in mass (Figure 1A):

$$p_{\text{capture}} = .078 + (.5 \times 10^{-8} \times e^{1.4 \times \text{Mass}}) \tag{1}$$

The probability of being killed by a predator per 20 min was:

$$p_{\text{kill}} = \alpha \times p_{\text{capture}} \tag{2}$$

We also tested whether the near-linear relationship from Lima (1986) generated results different from our baseline model.

Energetic gain

We used prey encounter rates and food-item caloric values from field data on small parids (Brodin, 1994; Pravosudov, 1983, 1985) to calculate the probability of encountering a food item and the mean foraging success (food found during foraging can be either eaten or cached) from a foraging bout. Variability in prey encounter rate was simulated using a truncated normal distribution. When a bird decided either to feed or to cache during any given 20-min time interval when it is foraging, it could find from zero to six food items with a mean of three items. Each item was equal to 0.064 g of fat that a bird could gain from eating the item, thus three items generated 0.192 g of fat gained/20 min (based on Brodin, 1994; Pravosudov, 1983, 1985) and some specified variance between zero and 0.02 with the baseline variance of 0.01. We varied the value of each item from 0.047 to 0.080 g of fat (generating a mean foraging return of 0.14 to 0.24 g of fat per 20 min) to test how changing mean energetic gain affects the result of our model.

Table 4

Effect of overnight air temperature (°C) on maximum number of caches and daily probability of deaths

	Food caching birds		Non-caching birds
Temperature °C	Number of caches	Probability of death/ 24 h ($\times 10^4$)	Probability of death/ 24 h ($\times 10^4$)
−5 (baseline)	30.05 ± 2.77	7.07	8.08
−10	37.08 ± 3.53	7.11	9.29
−15	46.06 ± 4.57	8.41	11.15

Daytime temperature was −5°C for all condition.

We assumed that mean energy gain from cache retrieval is a function of number of existing caches: the more existing caches the higher the return. The logic behind this is as follows: parids have fairly large territories (up to 50 ha for Siberian tit; Pravosudov, 1987; 4–5 ha for Carolina chickadees, personal observation) and these birds are scatterhoarders. If a bird has only a small number of caches when it decides to retrieve them, it might be far away from these caches and it would take more time and energy to retrieve them thus making the mean return smaller. At higher cache densities, cache retrieval should be more rapid and the mean energetic reward from retrieval should correspondingly increase. The function we used to calculate the mean energetic gain from retrieval per 20 min time unit is (see Figure 1B):

$$\gamma_R = \begin{cases} N_{\text{ret}} \times M_{\text{ret}} \times (1 + 0.2 \times (1 - e^{-0.025 \times \text{CS}})), & \text{if CS} > N_{\text{ret}} \\ \text{CS} \times M_{\text{ret}} & \text{otherwise} \end{cases} \tag{3}$$

Where γ_R = mean retrieval gain measured in g of fat/20 min, $N_{\text{ret}} = 5$ = zero intercept of retrieval function (measured in number of items retrieved), $M_{\text{ret}} = 0.064$ = value of one retrieved food item (g of fat), and CS = number of individual caches.

The bird can retrieve an average from five to six ($= 1.2 \times N_{\text{ret}}$) items per 20 min ($M_{\text{ret}}$ converts this into g of fat gained from eating this food) if it has more than five food items cached. If fewer than five items are cached, the bird simply retrieves all of them (i.e., $\text{CS} \times M_{\text{ret}}$). The shape of the curve is determined by the function ($1 - e^{-0.025 \times \text{CS}}$). Thus, we assumed that energetic gain from cache retrieval is 1.7 to two times larger than the mean energetic gain from foraging (0.192 g of fat/20 min). Some other models used either smaller (Brodin, 2000; Brodin and Clark, 1997) or larger (McNamara et al., 1990) ratios of retrieved gain to foraging gain.

Under the baseline conditions, we assume a zero variance in energetic gain from retrieval. We also varied the variance in energetic gain from retrieval to test the sensitivity of the model to this parameter. Variance in retrieval gain was incorporated in the model using a truncated normal distribution of N_{ret} with a mean equal to 5 and a variance ranging from 0 to 0.02.

Cache loss

For the baseline conditions, we assumed that pilferage rates were constant during the entire 24-h of each day and that the combination of pilferage and forgetting cache locations re-

Table 5

Effect of cache half-life on mass, maximum number of caches and daily probability of death

Cache half-life	Morning mass (g)	Evening mass (g)	Number of caches	Probability of death/ 24 h ($\times 10^4$)
2.5 days	9.55 ± 0.12	10.33 ± 0.13	0.0	8.08
5 days	9.02 ± 0.14	9.78 ± 0.14	18.44 ± 2.79	7.97
10 days	8.74 ± 0.09	9.48 ± 0.10	27.50 ± 2.90	7.40
20 days (baseline)	8.70 ± 0.08	9.44 ± 0.08	30.05 ± 2.69	7.07

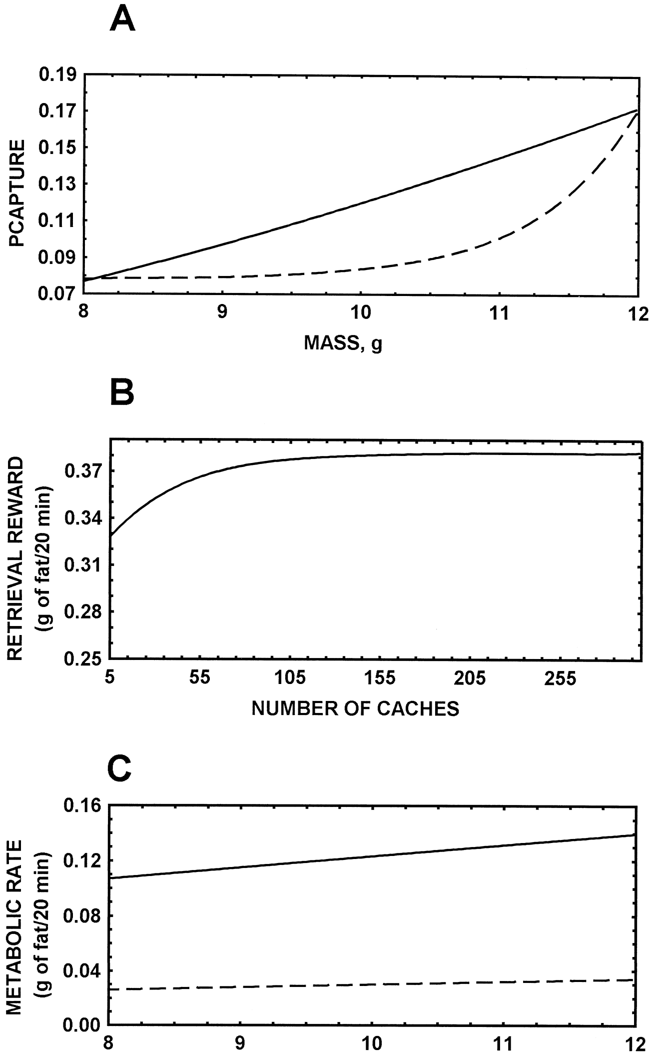

Figure 1
(A) Relationship between a probability of being captured after an attack occurs (p_{capture}) and body mass. Solid line represents Lima's (1986) equation and broken line represents the equation used in our baseline model. (B) Mean gain from retrieving caches as a function of number of caches, starting at the mean retrieval rate of five caches per 20 min, (C) Broken line represents metabolic rate of resting birds and solid line represents metabolic rates of active (foraging and eating, foraging and caching, retrieving) birds as a function of body mass.

sulted in a 50% loss ("half-life") of the cache in 20 days. There is some debate about the true pilferage levels in the field (Lucas and Zielinski, 1998). Some authors argue that caches last only a few days (Sherry et al., 1982; Stevens and Krebs, 1986). In contrast, Brodin (1994) suggested that these high pilferage rates measured in the field result from a bias caused by providing food at feeders. The 20-day half-life is a figure Brodin (1994) measured in a Swedish population of willow tits. We tested the effect of cache loss rates on the results of our model by varying the cache's half-life from 20 to 2.5 days.

Note that we assume that animals that forget or lose their caches do not increase food encounter rate (in contrast to Brodin and Clark, 1997; Smulders, 1998).

Metabolic costs

Mass-dependent basal metabolic costs were taken from Lucas and Walter (1991) and scaled for 20-min time intervals:

$$\text{BMR} = 0.00616 \times \text{MR}' \times (\text{Mass}/1000)^{0.66} \qquad (4)$$

where

BMR = basal metabolic rate measured in g of fat lost per 20 min (for conversion of metabolic rate into g of fat we assumed that a gram of fat is equivalent to 37716 J [Chaplin, 1974; Lucas and Walter, 1991]), Mass = body mass of a bird in g, and

$$\text{MR}' = 45.65 - (1.33 \times \text{Temperature}),$$

$$\text{with ambient temperature measured in °C.} \qquad (5)$$

All justifications for the BMR equation are presented in Lucas and Walter (1991). Note that Equation 4 incorporates the effect of higher fat loads (higher body mass) and that this mass-dependent basal metabolic rate is one of the two modeled fat maintenance costs (the second cost is mass-dependent predation risk described above).

To calculate the metabolic cost of different activities, we used multiples of the BMR:

$$\text{MR}_{\text{forage and eat}} = 8.0\text{BMR}, \qquad (6)$$

$$\text{MR}_{\text{forage and cache}} = 8.0\text{BMR}, \qquad (7)$$

$$\text{MR}_{\text{retrieve caches}} = 8.0\text{BMR}, \qquad (8)$$

$$\text{MR}_{\text{rest}} = 1.95\text{BMR}, \qquad (9)$$

$$\text{MR}_{\text{rest at night}} = \text{BMR}. \qquad (10)$$

Using doubly-labeled water, Carlson and Moreno (1992) showed that the cost of short flights, routinely used by parids during foraging, can be as high as 12 times night-time BMR. Thus, we think that our estimation of MR of any activity that usually involves short flights including foraging, caching and retrieving food caches is reasonable. The figure for resting metabolic rate (1.95BMR) is from Weathers et al. (1984) and

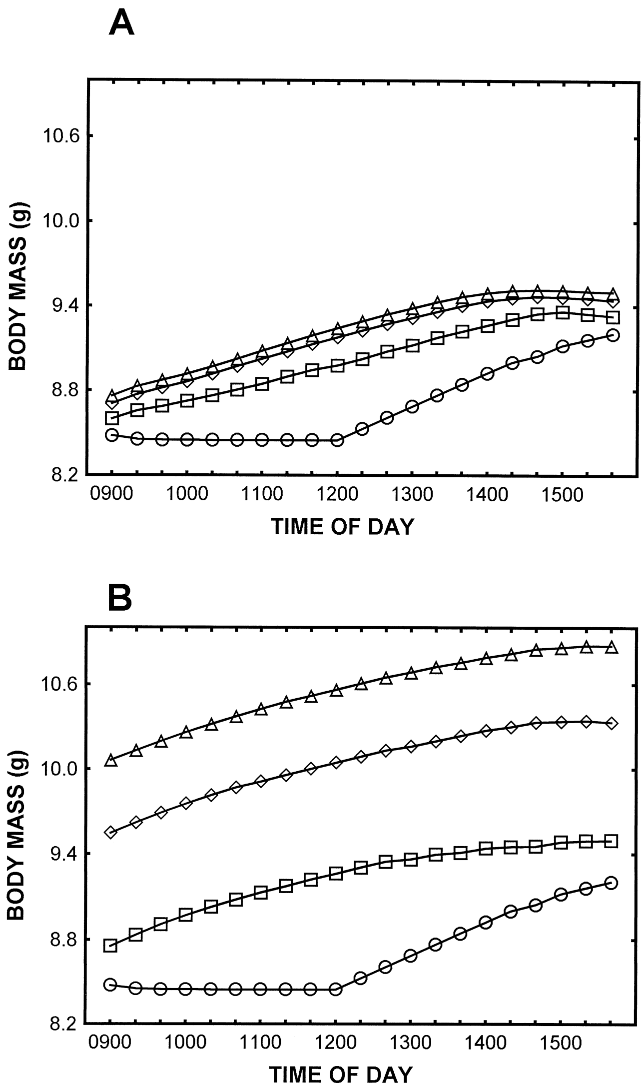

Figure 2
Optimal daily patterns of fat reserves (expressed in body mass) of cachers (A) and non-cachers (B) at four levels of variance in foraging success. Circles: $\sigma^2 = 0$, squares: $\sigma^2 = 0.004$, diamonds: $\sigma^2 = 0.01$, triangles: $\sigma^2 = 0.02$.

Buttemer et al. (1986). Figure 1C presents values of metabolic rates for the range of energy reserves considered in the model.

For the baseline calculations, ambient temperature was constant at −5°C both day and night. Since nocturnal temperature is often lower than diurnal temperature, we tested the effect of varying night temperature from −5 to −15°C.

RESULTS

Effect of variability in foraging success: comparison of food-caching and non-caching birds

Almost no caching is expected when there is no variability in foraging success (Table 1). As a result, daily patterns in the size of fat reserves for caching birds are identical to those of non-cachers: both groups were predicted to maintain their morning body mass until midday followed by a steady increase until dusk (Figure 2). Thus when foraging success is certain, the birds minimize the cost of acquiring and maintaining energy reserves early in the day. In the afternoon, the birds gain energy needed for overnight survival by eating virtually all encountered food.

At any appreciable level of variance in foraging success, the daily patterns of fat reserves change significantly compared to the hypothetical no-variance condition. When foraging success is stochastic, the birds are expected to gain mass more rapidly in the first part of the day slowing down toward late afternoon (Figure 2). The most striking result here is that, contrary to previously published predictions (McNamara et al., 1990), caching and non-caching birds are predicted to maintain qualitatively similar daily patterns in the regulation of fat reserves (Figure 2). Indeed, both groups of birds are predicted to gain similar amounts of fat over the course of the day (Table 2). With an increase in variance in foraging success, both caching and non-caching birds are predicted to increase the absolute size of their fat reserves as a hedging strategy against increased risk of starvation. The increase in absolute mass, however, is much higher in non-caching birds since they have only one option (increasing their fat reserves) to hedge against unpredictable foraging conditions. In caching birds, the relatively lower size of fat reserves is compensated for by an increase in cache size when foraging success becomes more variable (Table 1).

With zero variance in foraging success, feeding rates are predicted to be low early in the day, then peak in mid afternoon (Figure 3), a pattern reflecting the optimal daily mass trajectory (Figure 2). In contrast, at the higher levels of variance in foraging success, birds are predicted to eat most actively during the first part of the day (Figure 3). Activity is minimal just before roosting (Figure 3) causing mass to level off and even decrease slightly at that time (Figure 2). These daily patterns in feeding gains are similar for both caching and non-caching birds (Figure 3).

At all levels of variance in foraging success, food-caching birds are predicted to cache food primarily in the morning and retrieve caches primarily in the evening. There is also a small peak in morning retrieval (Figure 4). These patterns derive from the trade-off between risk of starvation and risk of predation. Birds should cache early in the day when time is not limited, and when this activity can be performed at low mass levels (and therefore at lower predation risk). Mass levels must increase by dusk in order to meet nocturnal metabolic expenditures. Retrieval could be crucial when foraging has failed to provide enough energy to meet energetic costs. This is particularly true late in the day when foraging time is limited. However, food-caching birds get most of their energy from foraging and food caches constitute only a small part of their daily diet, even at the highest level of variability in foraging success (Figures 3 and 4). Nonetheless, probability of death of cachers at high levels of variance in foraging success is considerably lower than probability of death of non-cachers (Table 2). This result suggests that under the baseline conditions, caches are used only when feeding is not successful, and the strategic use of cached food can substantially decrease mortality rates.

Effect of food availability on energy reserves of food-caching birds

Increasing mean foraging success by 12.5% over the baseline condition (0.22 g of fat/20 min) generates almost no changes in predicted fat reserves (Table 3). However, the increase in foraging success generates a reduction in cache size and a reduction in probability of death (Table 3). A further increase to 25% over the baseline (0.24 g of fat/20 min) has a similar effect (Table 3). Higher foraging success reduces starvation risk and thus decreases the value of cached food. When the mean foraging success was decreased by 12.5% below the base-

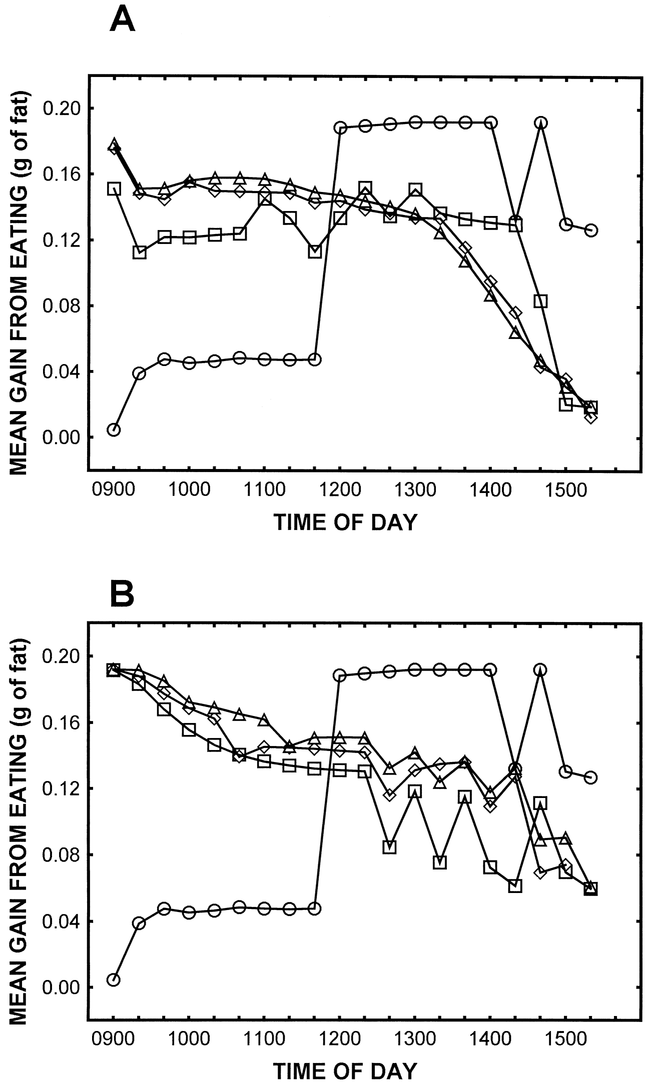

Figure 3
Optimal daily patterns in mean feeding gain of cachers (A) and non-cachers (B) at four levels of variance in foraging success. Circles: $\sigma^2 = 0$, squares: $\sigma^2 = 0.004$, diamonds: $\sigma^2 = 0.01$, triangles: $\sigma^2 = 0.02$.

line value (0.17 g of fat/20 min), birds were predicted to increase their fat reserves only slightly while greatly increasing their number of caches (Table 3). The most interesting result here was that the optimal daily pattern of caching activity changed dramatically when mean foraging success was reduced below the baseline: birds were predicted to cache almost all day with a peak in the evening (Figure 5) as opposed to the peak in the morning predicted for all other conditions tested. The shift in daily caching pattern results from a shift in time budget, especially a decrease in resting. In general, resting reduces predation risk at the cost of the lack of energetic intake. This tradeoff is not adaptive when birds must expose themselves to predation risk more in order to avoid starvation, a condition that is met in our model with a reduction in mean foraging success by 12.5% below baseline. Under these conditions, a bird is most likely to eat early in the day, and show increased caching, resting and retrieval late in the day (Figure 5). Late in the day, a bird will retrieve at the low body mass, eat at intermediate mass and cache if it is relatively heavy (data not shown).

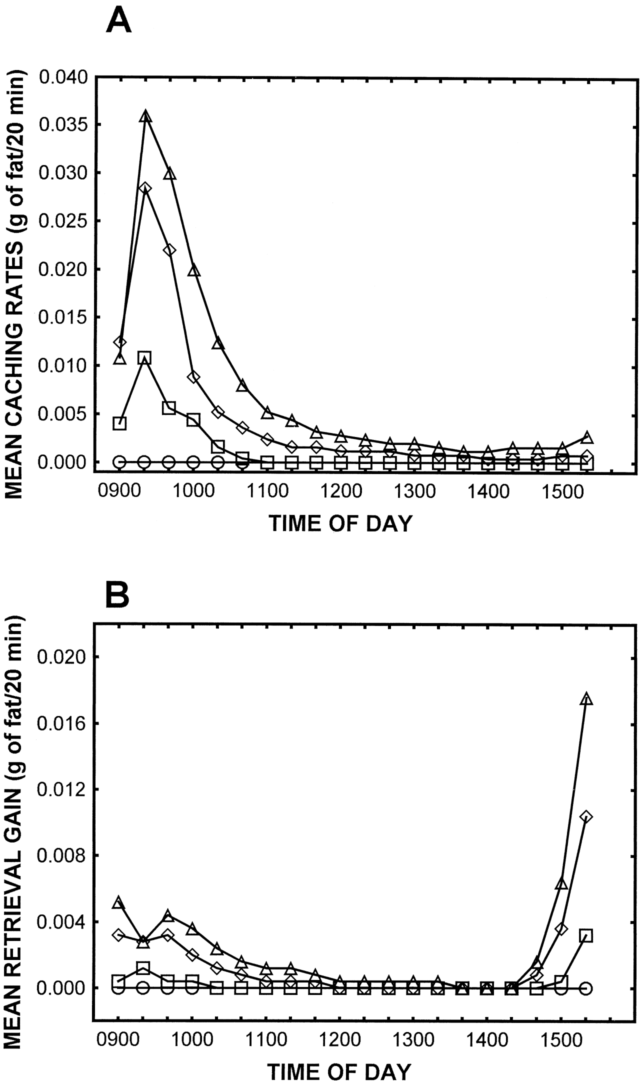

Figure 4
Optimal daily patterns of caching (A) and retrieving (B) at four levels of variance in foraging success. Circles: $\sigma^2 = 0$, squares: $\sigma^2 = 0.004$, diamonds: $\sigma^2 = 0.01$, triangles: $\sigma^2 = 0.02$.

Optimal daily retrieval patterns were similar for a wide range of foraging conditions (i.e., with both increased and decreased gain compared to baseline conditions) with a large peak in the evening and a small peak in the morning (Figure 5). Under reduced foraging success, retrieved caches represented a larger part of the diet during the evening compared to the baseline conditions (Figure 5). Finally, a reduction of foraging success to 25% below baseline (0.14 g of fat/20 min) results in an extremely high probability of death (Table 3).

Effect of lower temperature at night

For simplicity, in our baseline model we considered ambient temperature to be constant at −5°C. Since air temperature during the night is usually lower than during the day, we tested the model with a nocturnal temperature of either −10°C or −15°C. We did not address the issue of hypothermia (e.g., Reinertsen and Haftorn, 1986), because we have shown previously that use of nocturnal hypothermia should not affect the daily mass patterns (Pravosudov and Lucas, 2000). In food-caching birds, lower temperature at night results in high-

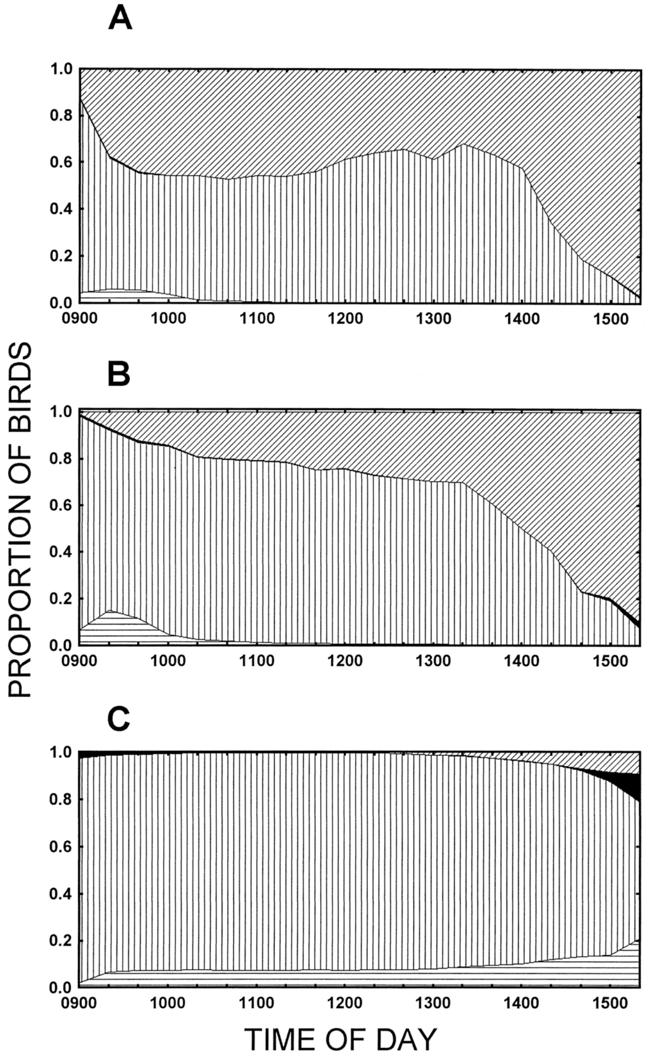

Figure 5
Proportion of birds predicted to be engaged in each available type of behavior as a function of time of day. Horizontal hatching—caching, vertical hatching—eating, black—retrieving, and right hatching—resting. A: gain = 0.22 g of fat/20 min, B: gain = 0.19 (baseline), C: gain = 0.17.

er fat reserves before roosting but there was almost no change in morning mass (Figure 6). The birds are predicted to gain just enough mass to compensate for higher losses during the night. The optimal daily mass patterns were not predicted to change qualitatively, but birds were predicted to gain more mass in the first part of the day when ambient temperature at night was lower (Figure 6). Optimal number of maintained caches was predicted to increase with the higher nighttime energy demands (Table 4). Non-caching birds, on the other hand, were predicted to increase both morning and evening fat reserves (Figure 6). Reducing nighttime temperature affects probability of death more in non-caching birds (Table 4; 38% increase from −5 to −15°C) than in caching birds (21% increase).

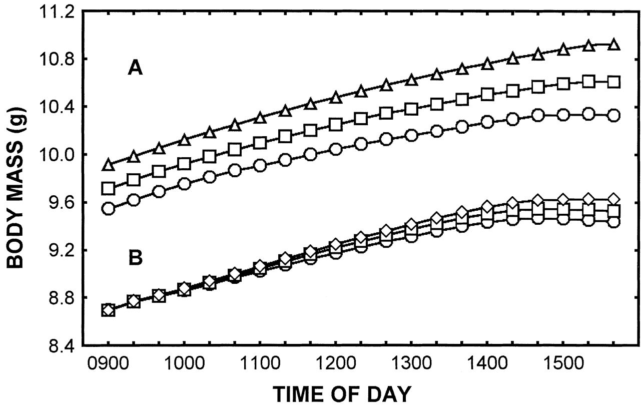

Figure 6
Optimal daily body mass trajectories of non-caching (A) and caching (B) birds at three levels of overnight air temperature. Circles: −5°C (baseline), squares: −10°C, and triangles: −15°C.

Effect of higher metabolic cost of resting

For the baseline model, we assumed (following Lucas and Walter, 1991) that the metabolic cost of any activity is almost four times higher than the metabolic cost of resting (Figure 1). However, McNamara et al. (1990) assumed no difference in metabolic costs between activity and inactivity for their baseline model, so we tested whether these assumptions affected the results of our model. If we increased the metabolic cost of resting from 1.95 BMR to 8.0 BMR (MR of any activity), there is no qualitative change in the predictions and only a small change in predicted levels of energy reserves: fat reserves decreased by 2%, number of caches increased by 14%, and probability of death increased by 22% compared to the baseline.

Effect of cache half-life

A reduction in the half-life of the cache had a profound effect on energy management in caching birds. Number of caches was smaller at 10 days half-life and caching ceased almost completely at 2.5 days cache half-life (Table 5). The predicted level of fat reserves and probability of death also increased with a decrease in cache half-life (Table 5).

Effect of mean energetic gain from cache retrieval

If we double potential retrieval rates by increasing the value of N_{ret} (unconstrained minimal number of retrieved items per 20 min) from five to 10, almost no changes were predicted in the levels of fat reserves compared to the baseline conditions (Figure 7A). However, at this value of N_{ret} number of caches was predicted to decrease by 22%. When we increased N_{ret} to 39.0 (making retrieval gain 13 times larger than mean feeding gain as in McNamara et al., 1990), the optimal daily energy management patterns also were not predicted to change appreciably. At $N_{ret} = 39$, fat reserves were predicted to increase by 1.9% (compared to the baseline) and the optimal daily trajectory of body mass also remained unchanged (Figure 7A). Number of caches was predicted to be 28% smaller than that at the baseline conditions. Optimal daily caching routines were not predicted to change qualitatively (data not presented) and retrieval had a small peak in the morning and a large peak at the end of the day at all modeled conditions (Figure 7B). Thus, increasing only the mean energetic gain from retrieval has almost no effect on any of the patterns of interest.

Effect of variability in mean energetic gain from cache retrieval

For the baseline model, we used zero variance in mean energetic gain from cache retrieval (Figure 1B). Increasing the variance of retrieval gain to about half of the variance in for-

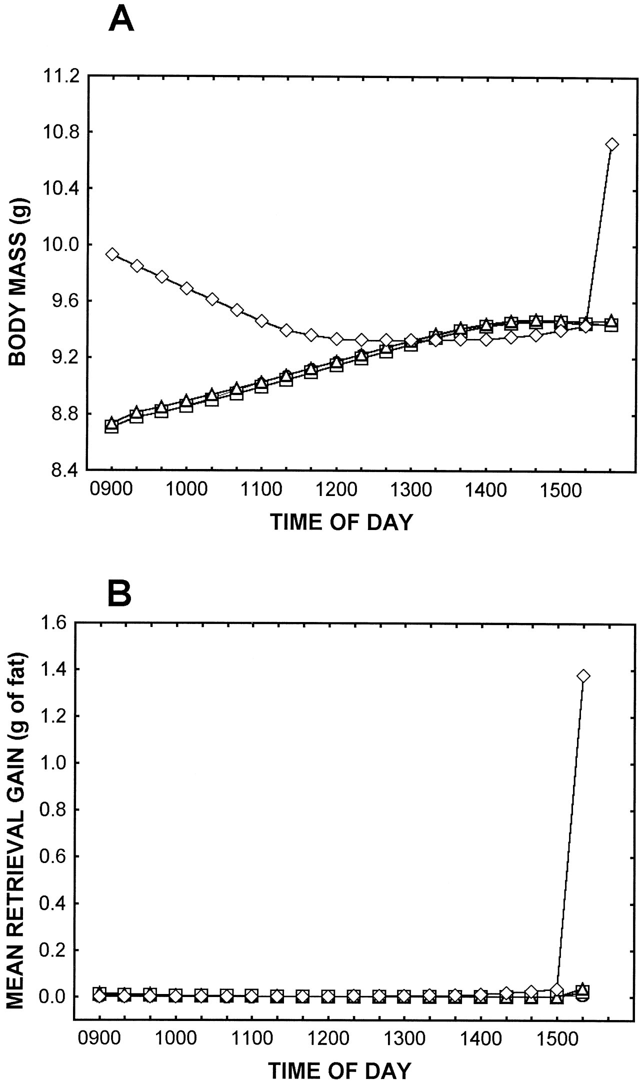

Figure 7
Optimal daily body mass trajectories (A) and retrieval return (B) at four levels of retrieval gain. Diamonds represent simulations similar to the McNamara et al. (1990) model in which probability of survival of caches during the day is one and all caches disappear overnight. All other simulations included cache loss with a 20-day cache half-life. Circles: $N_{ret} = 5.0$ (baseline), squares: $N_{ret} = 10.0$, triangles: $N_{ret} = 39.0$, diamonds: $N_{ret} = 39.0$ (simulation of McNamara et al. 1990).

aging gain (baseline) had almost no effect on the predictions. When the variance was increased further to that similar to the baseline variance in foraging success, number of caches was predicted to decrease and fat reserves to increase (data not presented). Since the variance in retrieval gain indicates an uncertainty in getting such a reward, this result suggests that when retrieval becomes more variable, it pays to invest more in fat reserves and less in caches.

Effect of the almost linear relationship between predation risk and body mass on model's predictions

For all of our calculations we assumed an exponential relationship between risk of predation and body mass. When we simulated almost linear relationship between risk of predation and body mass (as in Lima, 1986: Figure 1A) there were no predicted changes in all daily patterns of energy management (for daily mass trajectories see Figure 8A). The only predicted differences were in absolute levels of fat and number of caches: fat levels were predicted to decline by about 1% while number of caches was predicted to increase by about 12% at the baseline conditions with almost linear mass-dependent predation risk function.

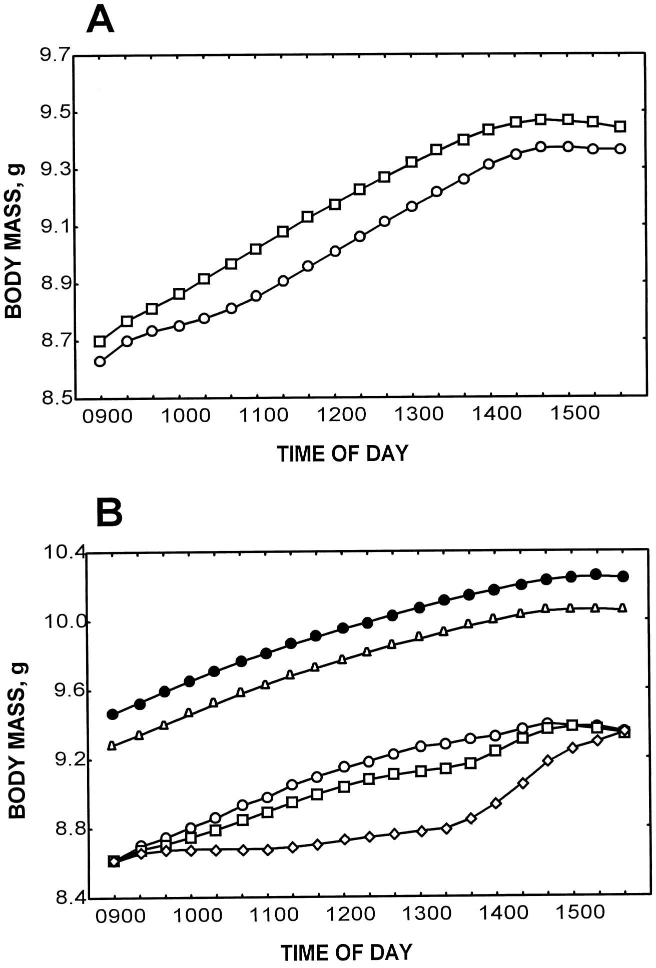

Figure 8
Optimal daily patterns of fat reserves (expressed in body mass) of cachers. A: open squares—baseline conditions, open circles—baseline conditions with the exception of mass-dependent predation risk function which is simulated after Lima (1983) and is almost linear. B: squares—exponential mass-dependent predation risk function, diamonds—almost linear mass-dependent predation risk function; for both squares and diamonds maximum number of caches is limited to 20 caches, mean foraging success is 0.24 g of fat/20 min, and $\sigma^2 = 0.02$. Open circles—exponential mass-dependent predation risk function, maximum number of caches is limited to 300 caches, mean foraging success is 0.24 g of fat/20 min, $\sigma^2 = 0.02$. Filled circles—maximum number of caches is limited to 20 caches, exponential mass-dependent predation risk function. Open triangles—maximum number of caches is limited to 20 caches, almost linear mass-dependent predation risk function; for both open triangles and filled circles mean foraging success is 0.19 g of fat/20 min and $\sigma^2 = 0.02$.

DISCUSSION

Our model supported some of the basic predictions of the previous dynamic models (Lucas and Walter, 1991; McNamara et al., 1990): birds should cache more food when: (1) foraging success becomes more variable, (2) mean foraging success becomes lower, and (3) overnight energy expenditures are increased. Our model also predicted that caching birds should carry less fat than non-caching birds. However, contrary to the results from McNamara et al. (1990), our model under baseline conditions predicted: (1) both caching and non-caching birds should increase their fat reserves more rapidly during the first part of the day slowing down toward late afternoon, and under a wide range of conditions there is no qualitative difference between cachers and non-cachers in their optimal daily mass trajectories (Figure 2), (2) caching occurs primarily in the morning (however, when mean foraging gain was small, birds were predicted to cache more in the evening), and (3) cache retrieval occurs mostly in the evening but there is also a small peak in the morning. These predictions fit the patterns observed in the field quite closely (Haftorn, 1989, 1992; Lilliendahl, 1997).

All of the predicted energy management strategies are a direct result of stochasticity of foraging built into the model. At any non-zero level of variance in foraging success, birds should hedge against resource shortfall by increasing their energy reserves. However, hedging strategies involve costs (Lima, 1986; McNamara and Houston, 1990): mass-dependent metabolic rate, mass-dependent predation risk, and higher predation risk when birds are foraging, caching or retrieving caches compared to birds that are resting. One well-known consequence of these costs is a foraging gain-predation risk trade-off that should cause the bird to regulate its energy reserves at lower levels when variance in resource abundance is low compared to conditions when variance is high (Bednekoff and Krebs, 1995; Ekman and Hake, 1990; Lima, 1986; Lucas and Walter, 1991; McNamara and Houston, 1990). In this respect, caching birds can maintain lower fat reserves than non-caching birds because food caches provide a high-return, low variance food source that can be built up when conditions are favorable (also see Hurly, 1992 and Hitchcock and Houston, 1994).

Optimal daily fat trajectories

Several different types of daily mass trajectory have been described in birds monitored in the field. For example, in willow tits, a food-caching parid, noon mass is significantly higher than morning mass (Haftorn, 1989, 1992), a result in line with both our predictions and those of Brodin (2000), but contrary to the predictions of McNamara et al. (1990). Haftorn (1992) also showed that diurnal mass patterns of caching parids were similar to those of non-caching parids; this is also predicted by our model. Hurly (1992) published daily mass trajectories of marsh tits (*Parus palustris*) under laboratory conditions. He suggested that the trajectories showed a delay in mass gain in the middle of the day similar to that predicted in McNamara et al. (1990). However, a closer analysis of the trajectories he published indicate that two birds (of four birds tested) exhibited a nearly linear increase in mass, and only one bird showed a decrease in mass at midday. Thus, these results are more in accord with the empirical data published by Haftorn (1989, 1992) than with the theoretical predictions from the McNamara et al. (1990) model. Lilliendahl (1997) published daily mass patterns of willow tits (a caching bird) and great tits (a non-caching bird); willow tits gained weight more rapidly in the morning, whereas great tits showed a more linear mass gain over the course of the day. Finally, in black-capped chickadees (*Poecile atricapillus*), a bimodal mass increase (morning and afternoon) but no midday decline has been observed (Graedel and Loveland, 1995).

Optimal daily eating routines

Under most parameter levels we simulated, our model predicted similar daily eating routines for caching and non-caching birds. When foraging success is variable, both groups of birds are predicted to eat most intensively in the morning and least intensively in the evening. For non-caching birds, similar feeding routines have been predicted by several previous models (e.g., Bednekoff and Houston, 1994a,b; McNamara et al., 1994). Such a pattern in feeding rates is caused, in part, by no foraging interruptions and high energetic requirements (McNamara et al., 1994), conditions that we have simulated here.

Optimal daily patterns of caching and retrieval

Under most parameter levels we simulated, our model predicted that birds should cache in the first part of a day and retrieve caches during the last part of a day. This result agrees with previous models (Lucas and Walter, 1991; McNamara et al., 1990). Our results disagree with the predictions by Brodin (2000), who suggested that when birds gain mass faster in the morning, they should cache in the middle of the day. This discrepancy between Brodin's (2000) model and our own are discussed further below.

When mean foraging success was low, our model predicted more intensive caching during the evening and less caching during the first part of a day (Figure 6C). This result suggests that the optimal daily routine of caching should be flexible and, in some instances, change with altered environmental conditions. Indeed, while many experimental studies showed a morning peak in caching (e.g., Lucas and Walter, 1991; McNamara et al., 1990), Hurly (1992) showed no consistent diurnal pattern and Pravosudov and Grubb (1997b) showed that birds tended to cache more during the later part of the day. Results from our model suggest that when foraging success is unpredictable and low, birds should not risk their future survival by spending time on caching during the morning. Instead, caching should be exhibited only after some insurance fat reserves have been accumulated.

Most of the retrieval falls in the later part of the day under the conditions we simulated. It seems that birds should retrieve caches only when it could be critical for them to obtain sufficient reserves in a short time. However, our model also predicted a small peak of retrieval in the morning when fat reserves are at their minimum. Morning retrieval has generally not been predicted by other models and it has not been observed frequently in the field. However, morning retrieval has been observed in some experimental studies (Pravosudov and Grubb, 1997b; but see Lucas and Walter, 1991) supporting our predictions. It seems that birds should use cached food only at critical times during the day: in the morning, when the fat reserves are lowest and risk of immediate starvation is high, and in the evening when it is crucial to reach some safe level of fat reserves to survive the night.

It is important to note that McNamara et al. (1990), Lucas and Walter (1991), and Brodin (2000) considered only short-term caching. Here we define short-term caches as those that are usually retrieved within 30 days of storage. However, short-term caching is not universal (Vander Wall, 1990). Boreal parids, such as Siberian (*Parus cinctus*) and willow tits (*P. montanus*) can cache tens of thousands of food items in autumn and retrieve these cached items several months later (Brodin, 1994; Haftorn, 1956; Pravosudov, 1985). This pattern is defined as a long-term caching behavior. Usually, when birds cache food intensively during autumn, almost no short-term retrieval occurs since food is plentiful (e.g., Haftorn, 1956; Pravosudov, 1985). Long-term caching strategies have been modeled by Brodin and Clark (1997) and Smulders (1998). However, even though boreal parids use long-term caching tactics in the fall, their caching patterns in the winter can be characterized as short-term (Pravosudov, 1983, 1985). In parids that occupy milder climates, for example Carolina chickadees (*Poecile carolinensis*), intensive autumnal caching during short periods has not been observed and they likely only cache food on a short-term basis (e.g., Lucas, 1994; Lucas and Walter, 1991). Indeed, short-term caching is characteristic of a variety of taxa occupying milder climates (VanderWall, 1990). Thus the caching patterns that we have modeled are a realistic description of energy management tactics of a fairly broad range of species.

The value of cached food

It is important to note that no field data have been published on the rate of energetic gain obtained from cache retrieval compared to the rate of gain from ordinary foraging. We assumed that such a value is about two times more than the mean gain from foraging. Brodin (2000) considered a range of values from 0.2 to 2.0. In their model of long-term caching, Brodin and Clark (1997) used a smaller ratio of retrieved versus encountered food energetic return. McNamara et al. (1990) assumed that birds could retrieve about 13 times more than the mean foraging gain. It is difficult to justify any of these assumptions other than to note that stomach capacity must limit how much a bird can physically consume (Bednekoff and Houston, 1994a). We can indirectly evaluate these assumptions by asking whether the model's predictions correspond to observed trends. One such prediction concerns the daily routine of body mass. Our predicted daily patterns of body mass match field observations (see Haftorn, 1989, 1992) better than previous models.

Our model predicted that birds should cache and retrieve a small amount of food compared to the food consumed during foraging. In agreement with this prediction, available field data on some boreal parids show that in the middle of winter these birds may cache about 10% of food they find (Pravosudov, 1983, 1985). However, even limited cache use is predicted to increase survivorship of caching birds (Table 2). Field data on the Eurasian nuthatch (*Sitta europaea*) showed that these birds retrieved caches mostly when conditions were bad and not under favorable conditions (Nilsson et al., 1993). This suggests that if caches are long-lasting, birds might only use them during critical periods, so even a small number of caches can enhance survival rates. Similar conclusions about the importance of limited cache use have been reached by Hitchcock and Houston (1994), who modeled cache use in acorn woodpeckers (*Melanerpes formicivorus*).

Longevity of caches

Another area for which we have inadequate field data is how long caches last (Lucas and Zielinski 1998). Cache loss can include natural loss due to pilferage, spoilage, and so on, and forgetting cache locations (Lucas and Walter, 1991). In our model, we assumed that if the location of an item is forgotten then the cached item does not add to the pool of food available for foraging. If we assumed that created caches increase overall food encounter rates, then caches created by one individual would be available to another individual which does not appear to be true (review Pravosudov and Grubb, 1997b). Our model predicted that unless cache half-life is more than 2.5 days, no caching should occur. Above this threshold, cache size should increase with an increase in cache longevity. Mortality rates also drop considerably with increased cache longevity. This result suggests that: (1) birds should not cache if caches are pilfered intensively, and (2) longer memory for caches promotes increased survivorship and increased reliance on cached food. When caches disappear at a high rate, birds should abandon caching and use fat reserves to hedge against stochastic foraging. Field and experimental data indeed suggest some parids retrieve their caches up to 48 days after storing them (Brodin, 1994), and that they can remember their caches for 28 days in experimental conditions (Hitchcock and Sherry, 1990).

Few experimental studies have evaluated the effect of pilferage on caching behavior. Hampton and Sherry (1992) showed that pilferage concentrated in one part of an aviary caused black-capped chickadees to alter their use of the high-pilferage area, but no data were presented on the effect of pilferage on caching rates. Kamil et al. (1993) showed that Clark's nutcracker (*Nucifraga columbiana*) similarly avoid pilfered sites. However, that study also did not ask whether pilferage affects caching rates. Clearly more work needs to be done on this issue.

The conclusions from our model differ from conclusions based on models developed by Brodin and Clark (1997) and Smulders (1998). Both previous models indicated that memory constraints would have little influence on the fitness of a caching animal. However, these models differ from ours in how they treat forgotten caches. In our model, forgotten caches are lost. In the Brodin and Clark (1997) and Smulders (1998) models, forgotten caches are still available to the bird and, more importantly, they increase future food encounter rate. The difference between the models makes the difference in predictions about the selective advantage of memory fairly transparent. Ecological conditions should dictate which set of assumptions is more realistic.

Energy expenditure

A previous model by Houston and McNamara (1993) predicted that for non-caching birds, increased energy expenditure should result in increased fat reserves as a result of hedging against higher metabolic costs. In caching birds, it was predicted that increased energy spent at night should result in larger fat reserves and larger number of caches (McNamara et al., 1990). Our model similarly predicted that in both caching and non-caching birds, a decrease in temperature overnight should result in fat levels elevated in the evening and caching birds were predicted to increase their number of caches. While non-caching birds were predicted to increase both morning and evening mass, as predicted by Houston and McNamara (1993), caching birds were predicted to increase their evening fat reserves only (Figure 6). It appears that while non-caching birds increase their morning fat reserves to insure that they can achieve a safe level of fat by the evening, caching birds should increase morning cache rate instead of increasing fat reserves. The relative fitness consequences of their use of caches in lieu of fat reserves is illustrated in the lower mortality rates of caching birds compared no non-cachers.

Haftorn (1992) argued that birds do not store food in the winter when energy expenditures at night are extremely high, because there is not enough food available to the birds. However, some parids do cache some of their food even in the middle of the winter (Pravosudov 1983, 1985), and the amount of caching observed (approximately 10% of all items found) is in general agreement with the amount of caching predicted by our model. Given that our model predicts no caching under very limited food access, the field results reported by Pravosudov (1983, 1985) imply that some parids may have sufficient resources to support caching behavior.

Finally, our model predicts that increased nocturnal energetic expenditures should actually cause an increase in caching rates, assuming that enough food is available. It would be interesting to know if food-caching birds living in less extreme conditions would cache more under such conditions.

The McNamara et al. (1990) model

Our model produced some results that are consistent with the results of the McNamara et al. (1990) model. Both models predict that variability in foraging success should result in increased number of caches and that non-cachers should carry higher levels of fat reserves than cachers (also see Lucas and Walter, 1991). However, the optimal daily patterns of fat reserves differ substantially between these two models. Why is there such a difference? We have already shown above that increasing the gain from retrieval of caches to 13 times larger than the mean gain from foraging (the value used in McNamara et al., 1990) does not change the optimal daily routines. If we add two additional assumptions used in the McNamara et al. (1990) model, complete loss of caches overnight and no disappearance of caches during the day, we get results similar to those of the McNamara et al. (1990) model (Figure 7). Now, fat reserves are predicted to decline from the morning until the last time interval during which the birds should increase mass by retrieving cached food. If we make gain from cache retrieval only two times larger than mean foraging gain, but assume overnight cache disappearance and no cache loss during the day, no caching was predicted. Thus, the daily patterns of body mass of caching birds described in McNamara et al. (1990) appear to result from a combination of assumptions which do not have strong empirical support: very high gain from cache retrieval, loss of caches overnight and no loss of caches during the day.

Brodin (2000) model

Brodin (2000) suggested that only a relaxation of the effect of mass-dependent predation risk (coupled with other assumptions discussed below) will produce a daily pattern of body mass in which hoarders gain more mass in the first part of the day (the ‘‘field-like’’ pattern), as opposed to the morning reduction in mass predicted by McNamara et al. (1990). Lucas and Walter (1991) came to the opposite conclusion: that the mass-dependent component of predation risk does not have a substantial effect on energy regulation. The discrepancy between these models appears to result from several assumptions.

Our results suggest that Brodin's (2000) conclusions are valid only if the maximum number of caches a bird can store and maintain is quite small. In his model, Brodin assumed a maximal number of caches of only 20 items (here scaled to our estimate of the value of each food item). In addition, our results suggest that the set of conditions that Brodin (2000) identified represent only a small subset of possible conditions causing a ‘field-like’ daily mass pattern. For example, we found no substantial difference in diurnal mass patterns predicted by our model at baseline conditions using exponential mass-dependent predation risk function compared with an almost linear mass-dependent predation risk function: in both simulation birds were predicted to gain most mass in the first half of the day, a pattern qualitatively similar to the ‘‘field-like’’ mass pattern (Figure 8A). If, like Brodin (2000), we reduced the maximum number of caches to 20 caches, our model predicted mass patterns very similar to ones predicted in Brodin (2000) with highest mass increase in the morning (Figure 8B). However, this pattern persisted whether we used a quadratic mass-dependent predation risk function or an exponential function similar to the function used by Brodin (2000) (Figure 8). In addition, Brodin (2000) suggested that this field-like pattern also results from cache retrieval being lower than the energetic gain from foraging. This assumption does not seem to be particularly robust: our model generates ‘‘field-like’’ daily mass patterns under baseline conditions where retrieval rates exceed foraging rates. The only conditions we could identify for which the shape of mass-dependent predation risk changed predicted daily mass patterns was an increased mean foraging gain coupled with a reduction in maximum number of caches (Figure 8B). We also obtained highest mass gain in the morning without limiting maximum number of caches to 20 caches, but by increasing mean energetic gain from feeding by 25% over the baseline. Thus, while we can verify Brodin's (2000) conclusions about the influence of the effect of mass-dependent predation risk on diurnal mass trajectories, our analysis adds two caveats to the conclusion. First, the result appears to rely on a fairly restrictive assumption about maximum number of caches. Second, in contrast to Brodin's (2000) conclusions, there is a broad range of additional conditions that generate the same predicted pattern irrespective of the shape of mass-dependent predation risk.

Thus, unless there is some extreme constraint in the maximum amount of food the birds can store, our analyses indicate that the different mass trajectories referred to by Brodin (2000), that is, ‘‘field-like’’ versus those from McNamara et al. (1990), do not derive from differences in the mass-dependent component of predation risk (see Lucas and Walter, 1991). Indeed, there is no single factor that dictates the relative shape of the diurnal mass trajectory. Mean levels of predation risk (as opposed to strictly mass-dependent risk) will clearly affect this pattern. The rate at which food is encountered and the variance in that rate also will affect the pattern. Even day length is an important component in the expression of diurnal mass trajectories (McNamara et al., 1994), although this has not been addressed in any of the models of caching behavior.

Finally, note that we assume that predation risk is the same for foraging birds and for birds retrieving cached food. Brodin (2000) assumed no predation risk while retrieving food. If we relax our assumption by reducing predation risk while retrieving to zero, our qualitative results are unchanged (data not shown). Thus, this prediction about the predation cost of cache retrieval is not the basis for the differences between our model and Brodin's (2000) model.

In conclusion, our model provides a general understanding of the factors that affect energy management strategies of organisms living in unpredictable environments. Factors that we considered in our model such as variability and availability of food supply, risk of predation, metabolic expenditure, and ambient temperature are critical elements of the optimization of energy management tactics for virtually all animals. While the details of ecological tradeoffs may vary from one species to the next (e.g., cost of carrying fat in flying and non-flying organisms could be different), we have continued the development of an integrated, multidimensional approach that will provide a general framework for the study of complex decision-making under realistic ecological conditions.

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