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ORIGINAL ARTICLE

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Daily patterns of energy storage in food-caching birds under variable daily predation risk: a dynamic state variable model

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Abstract Accumulating and maintaining sufficient energy reserves is critical for winter survival of birds. Because high fat levels are assumed to be associated with higher risk of predation, birds have been hypothesized to regulate their body mass as a trade-off between risk of starvation and risk of predation. Theoretical models of energy management in birds typically assume that predation risk is constant throughout the day. However, this important assumption has little empirical support, and there is some evidence suggesting that it might not always be correct and that predation risk may vary during the day. Because predation risk is a critical component of the predation-starvation trade-off, any change in its value through the day might have a profound effect on birds' optimal daily tactics of energy accumulation. We used a dynamic optimization model to investigate how changes in predation risk might affect birds' energy management decisions. Daily patterns of fat accumulation and feeding activity were predicted to change with predation risk in a manner consistent with previous models (lower mass gain and less feeding when predation risk is high). Our more counterintuitive results concern daily patterns of food caching and cache retrieval. When predation risk was assumed to peak at midday, birds were predicted to cache primarily in the afternoon and not in the morning even though predation risk was identical in the morning and afternoon. With other temporal patterns of predation risk, caching intensity was highest when predation risk was lowest. Surprisingly, the daily pattern of cache retrieval was predicted to be unaffected by daily patterns of predation risk: birds were always predicted to retrieve their caches primarily during the late afternoon with a small peak in the morning. Highest mortality was predicted with predation risk decreasing from morning to evening whereas lowest mortality was predicted with predation risk increasing from morning to evening. Our model helps explain large variations in observed daily patterns of energy management in birds and provides testable predictions that could help us understand the daily dynamics of predation risk and how birds should respond to it.

Keywords Predation risk · Energy management · Body mass · Food caches · Dynamic model · Dynamic programming · *Poecile* · *Parus* · Paridae · Foraging behavior · Caching behavior

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Introduction

During the non-breeding season, small resident passerine birds of temperate zones live in an environment characterized by unpredictable food supply, low ambient temperature, and short days. To increase their probability of survival in such conditions, wintering birds must accumulate and maintain sufficient energy reserves (McNamara and Houston 1990; Houston and McNamara 1993; Bednekoff and Houston 1994a, 1994b; Pravosudov and Grubb 1997a).

The main source of energy for birds is body fat and some species can also supplement fat with externally stored food caches. Highest possible fat reserves would minimize a bird's probability of starving to death. High fat loads, however, may be related to higher risk of predation from diurnal predators either through a reduction in maneuverability or through an increase in foraging time caused by increased metabolic demands (Lima 1986; McNamara and Houston 1990). Thus, optimal fat reserves are assumed to be regulated as a trade-off between the risk of starvation and the risk of predation. A question of how much energy a bird should accumulate and maintain under different ecological conditions has been a focus of many theoretical and empirical investigations (e.g., Ekman and Hake 1990; McNamara and Houston 1990; McNamara et al. 1990; Lucas and Walter 1991; Bednekoff and Houston 1994a, 1994b; Bednekoff and Krebs 1995; Pravosudov and Grubb 1997b; Brodin 2000; Pravosudov and Lucas 2000, 2001).

Almost all existing theoretical models of energy management in wintering birds assume that the risk of predation is constant throughout the day. Because predation risk appears to be a driving force in avian energy regulation, such an assumption may be critically important and may affect all predictions that concern daily patterns of energy accumulation and storage. To our knowledge, there is almost no empirical data on daily patterns of predation risk, and some available data demonstrate that daily predation risk may not always be constant throughout the day (Van der Veen 1999). Predation risk may be highest in the morning and in the evening when many crepuscular predators of small birds are active (e.g., Lima 1988). Knowing how birds would respond to varying risk of predation could provide a better understanding of optimal energy management in wintering birds and it could also help us understand the existing discrepancies between field data and theoretical models. For example, data on daily mass patterns in food-caching parids do not match the predictions of some dynamic models (reviewed by Pravosudov and Grubb 1997a). Brodin (2000) and Pravosudov and Lucas (2001) used dynamic models to investigate the basis of this discrepancy between theory and field data. However, different species may also have different daily patterns of energy accumulation at different times of year (reviewed by Pravosudov and Grubb 1997a) and published dynamic models do not provide a complete explanation for the variety of such patterns.

Here, we present results of a dynamic model of short-term energy management in small food-caching passerines such as parids in which we assume that predation risk is non-constant throughout the day, and discuss how changing predation risk might affect birds' energy management tactics. We used five possible scenarios with the same mean daily risk of predation: (1) constant predation risk, (2) predation risk increasing from morning to evening, (3) predation risk decreasing from morning to evening, (4) predation risk maximal in the morning and in the evening and lowest at midday, and (5) predation risk maximal at midday and lowest in the morning and in the evening.

Model

We developed a stochastic, dynamic state variable optimization model (Mangel and Clark 1988; Houston and McNamara 1999) with two state variables: fat reserves and food caches. The optimal state-dependent decision matrix was calculated assuming that birds maximize overwinter survival. The dynamic program calculates the behavior a bird should choose at all possible levels of fat reserves and number of caches throughout the day (McNamara et al. 1990; Lucas and Walter 1991). Once we had calculated the optimal sequence of decisions, we used a forward iteration to calculate probability distributions of number of caches and body mass at each time interval (Houston and McNamara 1999) and used these to find the mean daily patterns of body mass, eating, caching, retrieving intensities, and daily probability of dying. We initialized the forward iteration with a 10-g bird with 50 caches with a zero probability of any other mass and cache size combination. We then ran this iteration until the expected daily probability distributions of cache size and body mass had stabilized (see below). Varying this initial probability distribution had no effect on the equilibrium outcomes generated by the forward iterations. The results from the forward iteration can be conceptualized as generating a theoretical probability distribution of cache states and fat reserve states that a bird is expected to exhibit at any time during the day. Alternatively, it can be thought of as a description of a population of birds that follow the optimal decision matrix over the course of a day.

We modeled a small food-caching bird such as a black-capped chickadee (*Poecile atricapillus*) or willow tit (*Parus montanus*). We assumed that body mass ranges from 8.0 to 12.0 g (Lucas and Walter 1991; Lucas 1994) and that a change 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. Increasing the upper limit to 400 caches had no effect on the results of the model. We used a linear interpolation to estimate survival consequences of fractional increments for both fat reserves and cache size in the dynamic program. Linear interpolation was also used to calculate probabilities for the distribution of state variables in the forward iteration.

We divided an active day of 7 h (which approximately corresponds to day length in Stockholm, Sweden, in late November or Edinburgh, Scotland, in late December) 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 caches, or rest. We decreased the time interval to 10 min for several simulations and found no effect on the predictions. We 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 iterations equilibrated before 65 days. We therefore used this length as a conservative duration for all iterations. Each component of the model is first listed below and the dynamic optimization equations are presented in the Appendix.

Starvation risk

Following Lucas and Walter (1991), we assumed that the risk of starvation (F_s) was zero above some critical mass (10% of the maximum range in body mass or 8.4 g body mass). We used an incomplete beta function to calculate the probability of starvation below that mass. The incomplete beta function, $[I_x(a,b)]$, is similar to a cumulative normal distribution, although it has the realism of finite tails over the interval $0 \leq x \leq 1$; here x is the standardized body mass. The arguments (a,b) determine the relative shape of the curve. In our simulations, $a=b=3.3$, as in Lucas and Walter (1991).

Predation risk

We modeled diurnal predation risk as a two-stage process: the probability of a predator attack and the probability of depredation conditional on an attack occurring (as in Lima 1986; Lucas and Walter 1991; Pravosudov and Lucas 2001). When a bird is resting, its probability of being killed by a predator is zero. When a bird is active, there is some non-zero probability that the bird is attacked (α_{time}; see below). If attacked, the bird's probability of escape (P_{capture}) is mass dependent. Lima (1986) assumed an accelerating quadratic capture function, although the relationship he used is nearly linear over the range of mass we used in our model. Current empirical evidence (Kullberg et al. 1996; Kullberg 1998; Van der Veen and Lindstrom 2000) suggests that an accelerating capture function is more realistic than a linear function. We therefore chose an arbitrary function that has predation risk values similar to Lima's (1986) at the maximum and minimum mass levels we used in our model ($P_{\text{capture}}=0.078$ at mass = 8 g; $P_{\text{capture}}=0.173$ at mass=12 g), but also included accelerating risk with an increase in mass. We described the relationship between risk of predation and body mass as:

$$P_{\text{capture}}=0.078+(0.5\times10^{-8}\times e^{1.4\times\text{mass}}) \qquad (1)$$

The probability of being killed by a predator during one 20-min time interval is:

$$P_{\text{kill}}=\alpha_{\text{time}}\times P_{\text{capture}} \qquad (2)$$

To investigate the effect of predation risk changing through the day, we modeled five possible scenarios (note: in all cases, the numbers here represent the probability of attack in any given 20-min time interval during the day):

1. Constant predation risk:

$\alpha_{\text{time}}=6.7\times10^{-4}$.

2. Predation risk increases linearly from morning to evening

$\alpha_{\text{time}}=5.67\times10^{-4}+\{1.0^{-5}\times[(t-9)\times3+1]\}$,

where t is time of day in hours, starting at 0900 hours {note: $[(t-9)\times3+1]$ scales time to time in matrix units which range from 1 to 21}.

3. Predation risk decreases linearly from morning to evening

$\alpha_{\text{time}}=7.77\times10^{-4}-\{1.0^{-5}\times[(t-9)\times3+1]\}$.

4. Predation risk decreases linearly from morning to midday and then linearly increases to evening. Thus, the highest predation risk is in the morning and in the evening whereas the lowest predation risk is at midday.

For time from 0900 to 1220 hours:

$\alpha_{\text{time}}=7.67\times10^{-4}-\{2.0^{-5}\times[(t-9)\times3.0]\}$.

For time from 1220 to 1540 hours:

$\alpha_{\text{time}}=5.67\times10^{-4}+\{2.2^{-5}\times[(t-9)\times3.0-11]\}$.

5. Predation risk increases linearly from morning to midday and then decreases linearly from midday to evening. Thus, the highest predation risk is at midday and lowest in the morning and in the evening.

For time from 0900 to 1220 hours:

$\alpha_{\text{time}}=5.67\times10^{-4}+\{2.0^{-5}\times[(t-9)\times3.0]\}$.

For time from 1220 to 1540 hours:

$\alpha_{\text{time}}=7.67\times10^{-4}-\{2.2^{-5}\times[(t-9)\times3.0-11]\}$.

The mean daily probability of attack is the same for all five scenarios ($\bar{\alpha}_{\text{time}}=0.00067$), thus we are varying only the daily pattern and not the mean daily predation-risk level. In scenario 2 with predation risk increasing throughout the day, modeled predation risk is about 30% lower at the start of the day and 30% higher at the end of the day compared to the mean risk of predation. In scenario 3 with predation risk decreasing throughout the day, this pattern is reversed. In scenarios 4 and 5, the highest predation risk is 30% higher than the mean daily risk of predation and the lowest predation risk is 30% lower than the mean daily risk of predation.

Energetic gain

We based prey encounter rates and food item caloric values on field data from small parids (Pravosudov 1983, 1985; Brodin 1994a). Prey encounter rate is assumed to be identical irrespective of whether encountered items were eaten or cached. Variability in prey encounter rate is simulated using a truncated normal distribution. When a bird decided either to feed or to cache during any given 20-min time interval, it could find from zero to six food items with a mean of three items. Each item is equal to 0.064 g of fat, thus three items generate 0.192 g of fat/20 min (based on Pravosudov 1983, 1985; Brodin 1994a). We altered variance over the range of 0.004–0.016 per 20 min to evaluate how variance in energetic gain might influence the effect of changing predation risk on daily patterns of energy management.

We assume that mean energy gain from cache retrieval increases with cache size. This is simulated by assuming that the bird retrieves some base number of seeds (N_{ret}: assumed to be a truncated normal distribution with a mean of 5 and variance 0.01), and this base number of seeds increases as a function of the number of seeds cached (see Eq. 3 below). The logic behind this is as follows: parids are scatterhoarders with fairly large territories [up to 50 ha for the Siberian tit, *Parus cinctus* (Pravosudov 1987); 4–5 ha in case of Carolina chickadees (personal observation)]. If a bird has only a small number of caches when it decides to retrieve a cached item, it might be far away from any given cache location and require more time and energy to retrieve these caches thus making the mean return smaller than if the cache density were higher. We calculated the mean energetic gain from retrieval per 20-min time unit using the function

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

where

- γ_R=mean retrieval gain measured in g fat/20 min;
- N_{ret}=zero intercept of retrieval function (measured in number of items retrieved)=truncated normal distribution with mean 5 seeds per 20 min and variance 0.01;
- M_{ret}=0.064=value of one retrieved food item (g of fat);
- CS=cache size (number of individual caches).

A bird can retrieve an average of five to six (=$1.2 \times N_{ret}$) items per 20 min if it has more than five food items cached. This number of items is converted to grams of fat by multiplying by M_{ret}. The shape of the curve is determined by the function ($1 – e^{-0.025 \times CS}$). Thus, we assumed that energetic gain from cache retrieval is 1.7–2 times larger than the mean energetic gain from feeding (0.192 g of fat).

Cache loss

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 results in a 50% loss (“half-life”) of the caches in 20 days. There is some debate about the true pilferage levels in nature (Lucas and Zielinski 1998). Some authors argue that caches should last only a few days (Sherry et al. 1982; Stevens and Krebs 1986). In contrast, Brodin (1992, 1994b) suggested that these high pilferage rates measured in the field might result from a bias caused by providing food at feeders. The 20-day half-life is a value Brodin (1994b) measured in a Swedish population of willow tits. Finally, we assumed that forgotten or lost caches do not increase food encounter rate (in contrast to Brodin and Clark 1997; Smulders 1998).

Metabolic costs

Mass-dependent metabolic costs were taken from Lucas and Walter (1991) and Pravosudov and Lucas (2000, 2001) and scaled for 20-min time intervals:

$$\mathrm{BMR}=0.0062 \times \mathrm{MR'} \times (\mathrm{Mass}/1{,}000)^{0.66} \tag{4}$$

where:

- BMR=basal metabolic rate measured in g fat lost per 20 min;
- Mass=body mass of a bird (g);
- MR′=45.65–(1.33×Temperature), with ambient temperature measured in °C.

Equation 4 incorporates the effect of body mass that, along with mass-dependent predation risk, represents modeled mass-dependent maintenance costs.

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

- $\mathrm{MR}_{\text{forage and eat}}=8.0\times\mathrm{BMR}$
- $\mathrm{MR}_{\text{forage and cache}}=8.0\times\mathrm{BMR}$
- $\mathrm{MR}_{\text{retrieve}}=8.0\times\mathrm{BMR}$
- $\mathrm{MR}_{\text{rest}}=1.95\times\mathrm{BMR}$
- $\mathrm{MR}_{\text{rest at night}}=1.0\times\mathrm{BMR}$

Note that metabolic costs of all activities are mass dependent because they include mass-dependent BMR (Eq. 4).

Using double-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×nighttime BMR. Thus, we think that our estimation of MR of activities that involve short flights including foraging, caching, and retrieving food caches is reasonable. The figure for resting metabolic rate (1.95×BMR) is from Weathers et al. (1984) and Buttemer et al. (1986).

Day and night time ambient temperature was set constant at –5°C for all calculations.

Results

Predation risk decreases from morning to evening

Predicted patterns of diurnal mass regulation are strongly affected by diurnal patterns of predation risk. When predation risk is higher in the morning, birds should delay their mass gain early in the day and gain mass linearly in the afternoon at all levels of variance in foraging success (Fig. 1). In addition, birds facing higher morning predation risk should compensate for the delay in mass gain by maintaining a higher dawn (and dusk) mass, compared with birds on the increasing or constant predation risk schedules (Fig. 1). Eating activity should be lowest in the morning and highest in the afternoon, a pattern opposite to the daily eating pattern predicted for birds foraging under a constant or increasing risk of predation (Fig. 2).

Caching activity for birds faced with decreasing predation risk should also be lowest in the morning and highest in the afternoon, a pattern opposite to one for birds with constant or increasing predation risk (Fig. 3). Surprisingly, daily patterns of retrieval rates are predict-

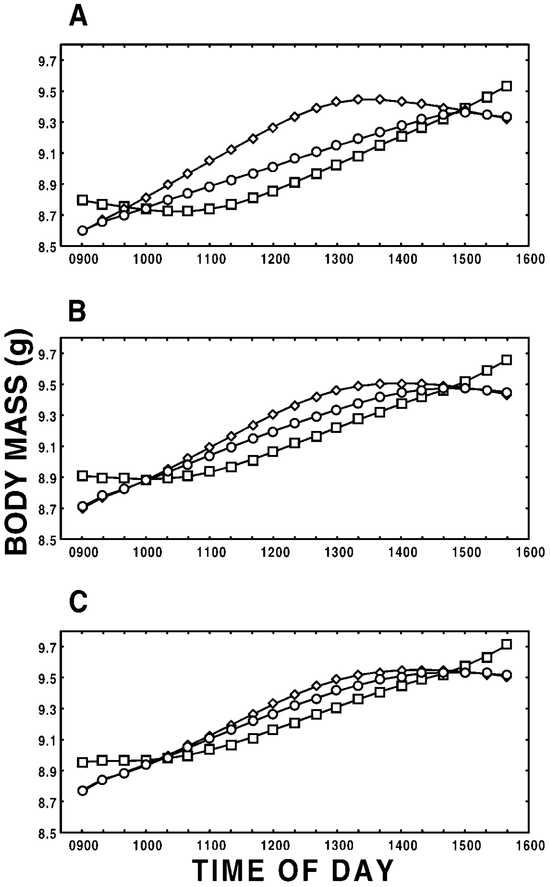

Fig. 1A–C Optimal daily patterns of fat reserves (expressed in body mass) in food-caching birds at three different patterns of daily risk of predation (*circles* constant risk of predation, *squares* risk of predation decreases from morning to evening, *diamonds* risk of predation increases from morning to evening) and at three levels of variance in foraging success (**A** σ^2=0.004; **B** σ^2=0.011; **C** σ^2=0.016)

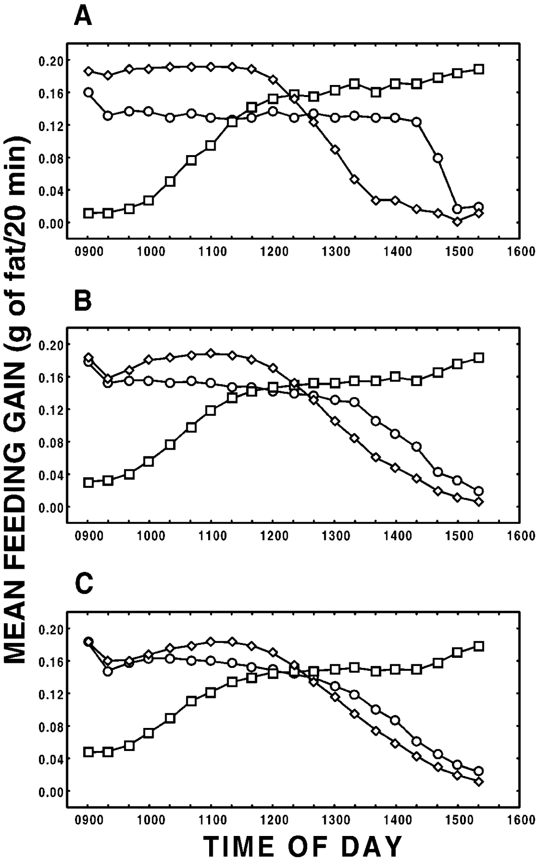

Fig. 2A–C Optimal daily patterns of mean eating gain in food-caching birds at three different patterns of daily risk of predation (*circles* constant risk of predation, *squares* risk of predation decreases from morning to evening, *diamonds* risk of predation increases from morning to evening) and at three levels of variance in foraging success (**A** σ^2=0.004; **B** σ^2=0.011; **C** σ^2=0.016)

ed to be similar for all three patterns of predation risk: cache retrieval is generally predicted to peak in the afternoon (Fig. 4), although the rate of retrieval is higher for decreasing predation risk than for the increasing or constant predation risk schedules.

Mean daily probability of death (from both starvation and predation) for decreasing and constant daily risk of predation is predicted to be similar (Fig. 5).

Predation risk increases from morning to evening

When risk of predation is higher in the evening, birds should accumulate mass earlier in the day compared to the other predation risk schedules (Fig. 1). Mass should also peak 2–3 h before the birds go to roost (Fig. 1). In addition, morning and evening mass under increasing risk should be similar to those during conditions of constant daily predation risk (Fig. 1).

Daily eating patterns are predicted to be similar under increasing predation risk to those modeled with constant predation risk, except that eating activity should be higher in the morning and lower in the evening when risk of predation is higher in the afternoon (Fig. 2). Daily food caching and retrieval patterns should also be similar to the ones modeled with constant daily risk of predation (Figs. 3, 4).

Mean daily probability of death should be lower for birds with daily predation risk increasing throughout the day compared with birds modeled with constant daily risk of predation (Fig. 5). Thus, predation costs imposed on morning foraging (our “decreasing predation risk scenario”) have stronger fitness consequences than predation costs on evening foraging (our “increasing predation risk scenario”). This prediction is not surprising because when foraging success is stochastic, birds try to gain most fat reserves in the first part of the day to decrease the probability of death from starvation. If predation risk is also highest during the first part of the day, birds can either shift their foraging activity toward afternoon which would increase their probability of death from starvation or continue foraging in the morning which would increase their probability of death from predation. When predation risk is highest in the evening, birds can

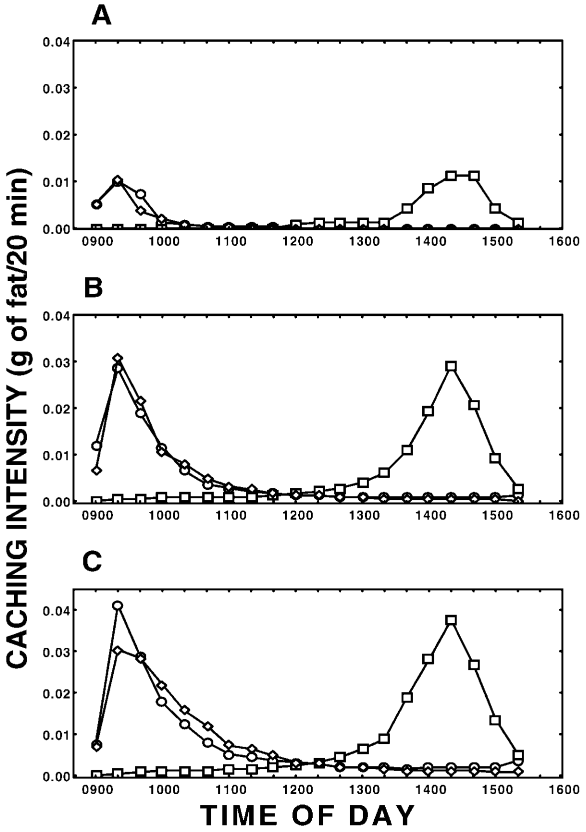

Fig. 3A–C Optimal daily patterns of mean caching rates in food-caching birds at three different patterns of daily risk of predation (*circles* constant risk of predation, *squares* risk of predation decreases from morning to evening, *diamonds* risk of predation increases from morning to evening) and at three levels of variance in foraging success (**A** σ^2=0.004; **B** σ^2=0.011; **C** σ^2=0.016)

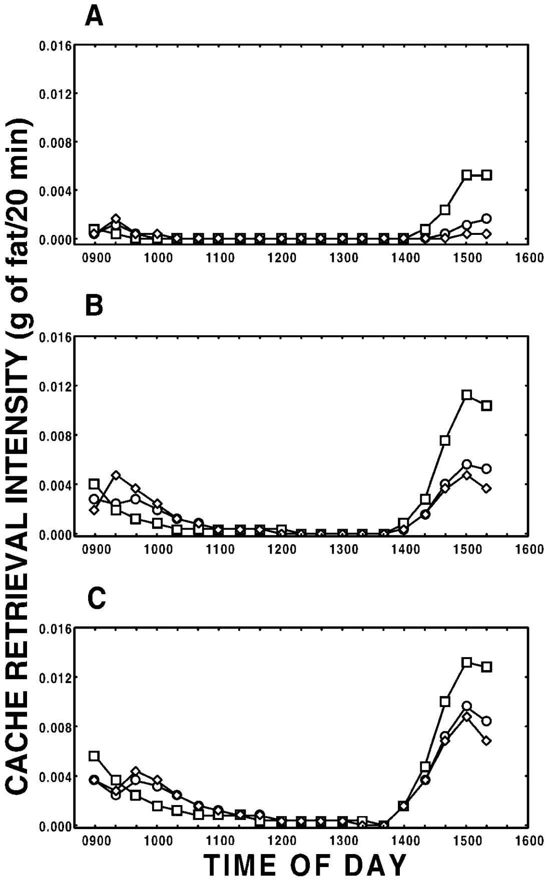

Fig. 4A–C Optimal daily patterns of mean retrieval rates in food-caching birds at three different patterns of daily risk of predation (*circles* constant risk of predation, *squares* risk of predation decreases from morning to evening, *diamonds* risk of predation increases from morning to evening) and at three levels of variance in foraging success (**A** σ^2=0.004; **B** σ^2=0.011; **C** σ^2=0.016)

gain most of their energy reserves earlier in the day when predation is low. By doing so, birds decrease both the probability of death from starvation and the probability of death from predation.

Non-linear change in predation risk

Not surprisingly, when predation risk peaks in both morning and evening, birds are predicted to slow their mass gain during the morning and evening hours whereas they should gain most fat reserves during the middle of the day compared to birds modeled with constant risk of predation (Fig. 6). Predicted mass gain during the morning hours strongly resembles mass patterns in birds modeled with predation risk decreasing from morning to evening whereas the mass gain during the late afternoon is quite different (compare Figs. 1, 6). In contrast, when predation risk peaks at midday, birds should gain mass primarily in the morning and in the evening with a plateau in the middle of the day (Fig. 6).

In contrast to previous scenarios where birds' daily eating activity was predicted to either increase or decrease from morning to evening, birds modeled with a

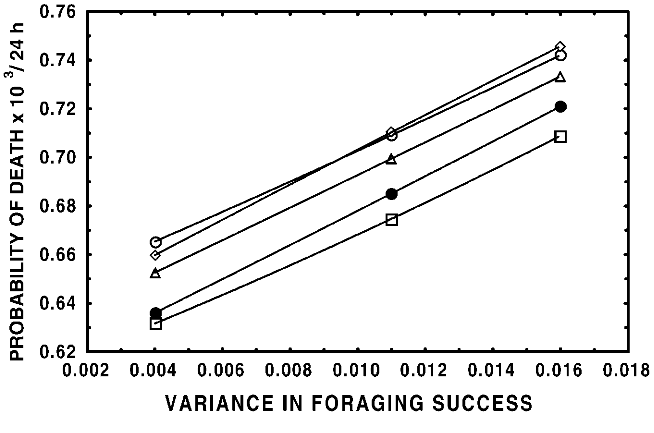

Fig. 5 Probability of death of birds at different daily predation risk patterns (*open circles* constant risk of predation, *open diamonds* risk of predation decreases from morning to evening, *open squares* risk of predation increases from morning to evening, *open triangles* risk of predation is highest at midday and lowest in the morning and in the evening, *filled circles* risk of predation is highest in the morning and in the evening and lowest during midday) at three levels of variance in foraging success

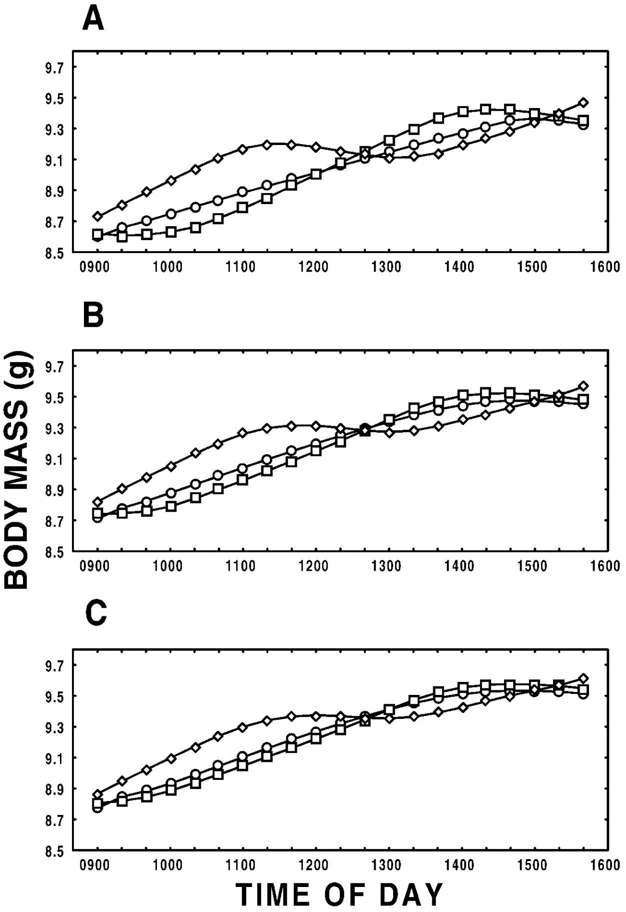

Fig. 6A–C Optimal daily patterns of fat reserves (expressed in body mass) in food-caching birds at three different patterns of daily risk of predation (*circles* constant risk of predation, *squares* risk of predation is highest in the morning and in the evening and lowest during midday, *diamonds* risk of predation is highest during midday and lowest in the morning and in the evening) and at three levels of variance in foraging success (**A** σ^2=0.004; **B** σ^2=0.011; **C** σ^2=0.016)

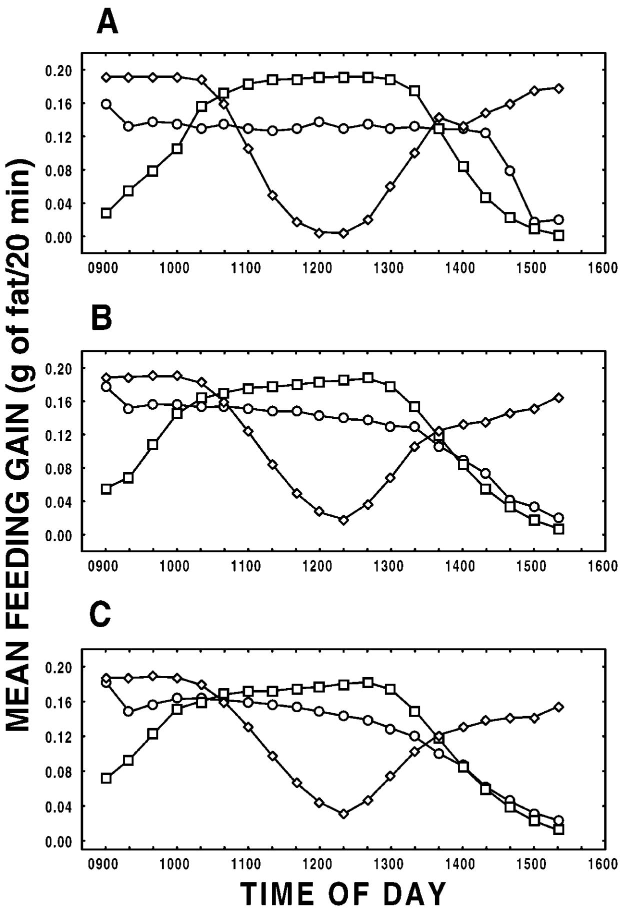

Fig. 7A–C Optimal daily patterns of mean eating gain in food-caching birds at three different patterns of daily risk of predation (*circles* constant risk of predation, *squares* risk of predation is highest in the morning and in the evening and lowest during midday, *diamonds* risk of predation is highest during midday and lowest in the morning and in the evening) and at three levels of variance in foraging success (**A** σ^2=0.004; **B** σ^2=0.011; **C** σ^2=0.016)

non-linear pattern of daily predation risk should have either a unimodal or bimodal peak in their feeding activity; when predation risk is highest in the morning and in the evening, birds should forage most intensively during the middle of the day. When predation risk is highest at midday, birds should eat most intensively in the morning and in the evening, with the greatest foraging effort in the morning (Fig. 7).

When predation risk is highest in the morning and in the evening, birds should cache food mostly during the middle of the day in sharp contrast to all other scenarios (Figs. 3, 8). When predation risk is highest at midday, birds should cache primarily during the afternoon, a pattern very similar to one predicted for birds with predation risk decreasing from morning to evening (Figs. 3, 8).

Cache retrieval patterns modeled with either predation risk highest in the morning and in the evening or at midday are predicted to be very similar: birds should retrieve most food during late afternoon with some retrieval during the morning (Fig. 9). The same pattern is predicted with predation risk either increasing or decreasing from morning to evening (Fig. 4).

When predation risk is non-linear, the probability of death falls between the two linear patterns of predation (Fig. 5). When risk of predation is highest at midday, probability of death is similar to one modeled with constant risk of predation or with risk of predation decreasing from morning to evening. When predation risk is highest in the morning and in the evening, probability of death is somewhat lower, although not as low as when predation risk increases from morning to evening.

Discussion

The results of our model indicate that qualitative changes in daily patterns of predation risk may cause wintering birds to change their daily energy management strategies. Energy management under decreasing diurnal pre-

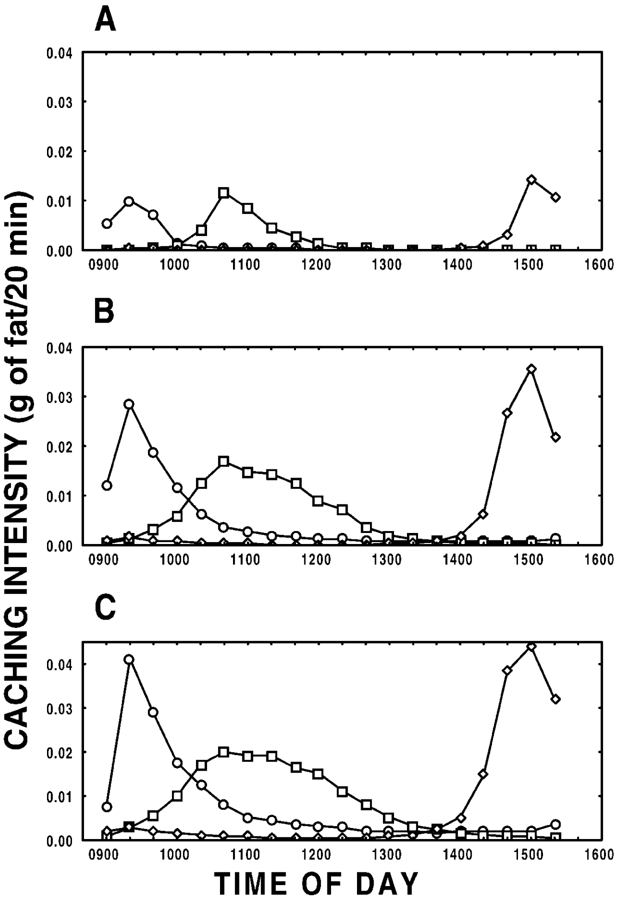

Fig. 8A–C Optimal daily patterns of mean caching rates in food-caching birds at three different patterns of daily risk of predation (*circles* constant risk of predation, *squares* risk of predation is highest in the morning and in the evening and lowest during midday, *diamonds* risk of predation is highest during midday and lowest in the morning and in the evening) and at three levels of variance in foraging success (**A** σ^2=0.004; **B** σ^2=0.011; **C** σ^2=0.016)

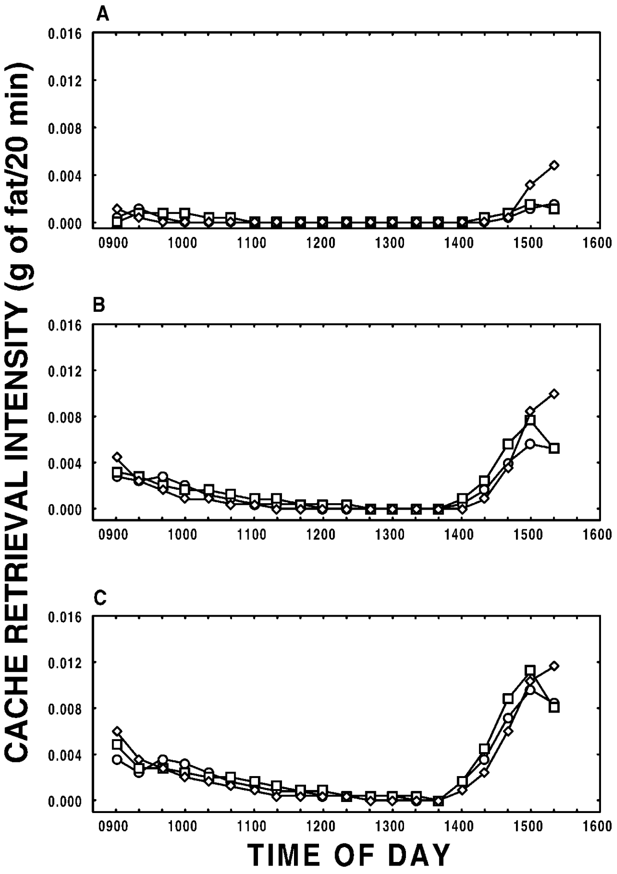

Fig. 9A–C Optimal daily patterns of mean retrieval rates in food-caching birds at three different patterns of daily risk of predation (*circles* constant risk of predation, *squares* risk of predation is highest in the morning and in the evening and lowest during midday, *diamonds* risk of predation is highest during midday and lowest in the morning and in the evening) and at three levels of variance in foraging success (**A** σ^2=0.004; **B** σ^2=0.011; **C** σ^2=0.016)

dation threat, when predation risk is highest in the morning and in the evening, and when predation risk is highest at midday is substantially different from energy management under constant threat. Energy management under increasing predation threat and under constant threat are predicted to be qualitatively similar. Under increasing threat, birds should gain fat more rapidly in the first half of the day and then lose some mass before going to roost, they should eat more in the morning and less in the evening compared to birds modeled under constant predation risk, and their caching and retrieval routines should be similar to those predicted for birds with a constant risk of predation. This scenario also predicts daily patterns of body mass very similar to ones observed in nature for food-caching parids (largest mass increase in the first part of the day; see Pravosudov and Grubb 1997a; Brodin 2000).

All the predicted patterns of energy management are driven by a starvation-predation trade-off. When risk of predation is higher in the morning, birds should wait to forage until later in the day when predation risk is reduced. However, this delay in foraging must be accompanied by an increase in dawn mass that provides sufficient energy reserves for the birds to survive the morning. This increase in dawn mass, in turn, results from an increase in dusk mass fueled by the shift in foraging to later in the day. When risk of predation is higher in the evening, it is more advantageous to gain all needed energy sources earlier in the day and to avoid high risk of predation by resting in the afternoon. When risk of predation is non-linear, birds should gain energy primarily when predation risk is low.

The diurnal pattern of predation risk will also affect mortality rates. Starvation risk is most strongly decreased by morning foraging. However, when predation risk is high in the morning, the birds are forced into one of two options. They can forage in the morning and thereby incur higher predation risk in order to reduce starvation risk. Alternatively, they can reduce morning foraging and as a result incur higher starvation risk in order to avoid predation. In either case, the result is a higher mortality risk when predation rates either decrease linearly throughout the day or when predation rates are maximal in the morning and evening (as opposed to maximal at midday).

The most interesting results predicted by our model concern daily patterns of food caching and cache retrieval. When predation risk is highest at midday, birds should have only one caching peak during the afternoon, although predation risk in the morning and in the afternoon are the same. Birds apparently need to gain enough fat reserves in the morning to allow for midday inactivity to minimize their risk of being killed by a predator. During the afternoon then, birds gain both fat reserves and build up their food caches.

Daily patterns of cache recovery are predicted to be relatively unaffected by daily patterns of predation risk and birds should always retrieve their caches in the later afternoon with a small peak in the morning. Retrieval patterns under the conditions we simulated appear to be driven primarily by the risk of starvation. If a bird has not accumulated enough reserves to survive the night, its last chance to survive is to retrieve caches before going to roost regardless of predation risk. The same logic explains the small peak of retrieval in the morning, especially when variance in foraging success is high. When a bird wakes up with very low fat reserves, it needs to get food immediately or it will not have enough energy to forage during the day. On the other hand, mass-dependent predation risk may prevent birds from accumulating safest levels of fat reserves during the day and, instead, birds store extra energy as food caches, usually in the first part of the day. In the evening, birds have highest fat loads and as a result their risk of being killed by a predator is highest. Retrieving caches at this time of day maximizes energy gain and minimizes risk of predation.

While there are quantitative differences in the predicted pattern of mass regulation for increasing predation risk and constant predation risk, the qualitative results are the same. Both patterns of predation risk should result in extensive morning feeding. This pattern has been discussed by several authors (e.g., Bednekoff and Houston 1994b; McNamara et al. 1994) and reflects the combined need to compensate for energy loss during the previous night and to store enough energy early in the day to offset impending energetic demands to be incurred during the rest of the day. Another similarity between constant and increasing predation risk arises from the fact that birds under constant predation risk experience higher predation risk in the evening because they are heavier in the evening and this increase in mass, in itself, will increase the risk of predation.

As variability in resource abundance increases, the mass trajectories of all modeled predation patterns converge. In effect, increased variance in food access increases the relative importance of starvation. Access to food in our model is assumed to be identical for all five predation patterns, thus an increase in variance in foraging success makes the models more similar by increasing the survival consequences of food acquisition in relation to the survival consequences of predation risk. Interestingly, this does not result in a convergence in either the diurnal eating pattern or in the diurnal caching pattern. This underscores an important aspect of energy regulation in caching animals: diurnal caching trajectories are more sensitive to environmental conditions than are diurnal mass trajectories (Lucas et al. 2001). This differential sensitivity is likely to be the basis for experimental evidence showing an effect of varying levels of resource variation on caching behavior but not on the regulation of body mass (e.g., Hurly 1992). It is also the basis for the use of caching behavior as a sensitive index of the "body mass set point" (i.e., the body mass animals regulate under ad libitum food access; see Fantino and Cabanac 1980).

The literature on daily risk of predation in nature is sparse. Van der Veen (1999) showed that the activity of diurnal predators in the Uppsala area, Sweden, was highest in the afternoon in December and February, whereas in November, there was no difference in predator activity between the first and second halves of the day. Bunn et al. (1995) documented a significant temporal reduction in the density of sighted red-tailed hawks (*Buteo jamaicensis*, a small-mammal predator), indicating a reduction in predation risk over the course of the day. By definition, crepuscular predators increase the risk of predation in the morning and evening compared to midday (Lima 1988). There might be several reasons why the risk of predation may change within the day during different seasons. For example, during the winter when the active day is short and foraging success could be highly variable, small avian predators may follow the same optimal strategy as small passerine birds by trying to gain most energy reserves earlier in the day.

The results of our model may help to explain a variety of described daily patterns of energy management in birds. For example, our model predicted that when the risk of predation is higher in the afternoon, birds should forage most intensively in the first half of the day and rest more in the afternoon. Data on yellowhammers (*Emberiza citrinella*) support such a prediction (Van der Veen 1999). Our model suggests that a change in the risk of diurnal predation might be responsible for many daily patterns of energy accumulation described for birds in the literature. For example, naturally foraging rock pipits (*Anthus spinoletta*) foraged more intensively late in the day during the winter whereas in spring and summer they fed more intensively in the morning (Gibb 1956). A higher risk of predation in the morning during the winter would explain the observed pattern. A pattern in which birds gain mass rapidly in the first half of the day and then reduce mass right before roosting time at night, observed in purple finches (*Carpodacus purpureus*; Bartleson and Jensen 1955), is consistent with the daily mass pattern predicted with risk of predation higher in the second half of the day. In tufted titmice (*Baeolophus bicolor*) maintained in a large outdoor aviary, observed daily patterns of energy accumulation were very similar to those predicted when risk of predation is highest in the morning and lowest in the evening (Pravosudov and

Grubb 1997b, 1998). These birds slightly delayed their mass accumulation in the morning, their feeding activity was lowest in the morning and highest in the evening, and they cached most food during the afternoon (Pravosudov and Grubb 1997b, 1998). McNamara et al. (1994) tried to explain a midday lull in foraging activity, but they did not look at daily patterns of predation risk. Our scenario with predation risk highest at midday would also explain such a pattern of foraging activity.

Daily predation risk is a critical component of birds' decisions on how to accumulate and maintain energy reserves throughout the day. Predicted daily patterns of energy management with variable predation risk could explain much of the variation in described patterns of avian body mass, feeding, and caching activity. More efforts are needed to investigate daily patterns of predators' activities to fully understand and explain birds' energy management tactics. Experiments in which predation risk is varied throughout the day are also needed to validate the assumptions of the model. Our model provides clear predictions of how birds should change their energy management tactics according to changes in predation risk. Investigating these tactics could also help to better understand daily activity of predators when direct observations are difficult or impossible.

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Appendix

Here we describe the equations used to calculate the optimal decisions. We assume that the birds maximize overwinter survivorship, conditional on their current state (mass and cache size) and the state change resulting from the optimal decision chosen at some time t. There are two components to the long-term survivorship [$P_s(D, t, \text{Mass}, \text{CS})$]: the probability of surviving both starvation risk and predation risk in the current time interval (SR; see below) and the probability of surviving from time t+1 to the end of winter [$P_s'(*, t, \text{Mass}, \text{CS})$]:

- $P_s(D, t, \text{Mass}, \text{CS})$=expected probability of survival resulting from a sequence of behavioral decisions, starting with behavior D exhibited during the present time interval (t) and followed by the best policy during all subsequent time intervals (from t to T, where T is the final interval), and conditional on current body mass (Mass) and number of caches (CS; as in Lucas and Walter 1991).
- $P_s'(*, t, \text{Mass}, \text{CS})$=expected probability of survival resulting from the sequence of optimal decisions, starting at time t and including all subsequent time intervals (as in Lucas and Walter 1991).

The equations for maximizing the survival probability are:

$$\begin{aligned} P_s(\text{eat}, t, \text{Mass}, \text{CS}) = {} & (1 - P_{\text{find}}) \times \text{SR}_{\text{eat}} \times P_s'(*, t+1, \Delta M_{nfe}, \\ & \Delta\text{CS}_{\text{nf}}) + P_{\text{find}} \times \text{SR}_{\text{eat}} \times \sum_{\text{nprey}=0}^{6} P_{\text{nprey}} \\ & \times P_s'(*, t+1, \Delta M[\text{nprey}]_{\text{eat}}, \Delta\text{CS}_{\text{eat}}) \end{aligned} \tag{5}$$

$$\begin{aligned} P_s(\text{cache}, t, \text{Mass}, \text{CS}) = {} & (1 - P_{\text{find}}) \times \text{SR}_{\text{cache}} \times P_s'(*, t+1, \\ & \Delta M_{\text{nfc}}, \Delta\text{CS}_{\text{nf}}) + P_{\text{find}} \times \text{SR}_{\text{cache}} \\ & \times \sum_{\text{nprey}=0} P_{\text{nprey}} \times P_s'(*, t+1, \Delta M_{\text{cache}}, \\ & \Delta\text{CS}[\text{nprey}]_{\text{cache}}) \end{aligned} \tag{6}$$

$$\begin{aligned} P_s(\text{retrieve}, t, \text{Mass}, \text{CS}) = {} & (1 - P_{\text{findcaches}}) \times \text{SR}_{\text{retrieve}} \\ & \times P_s'(*, t+1, \Delta M_{\text{nfr}}, \Delta\text{CS}_{\text{nf}}) \\ & + P_{\text{findcaches}} \times \text{SR}_{\text{retrieve}} \times \sum_{\text{nret}=0}^{10} P_{\text{nret}} \\ & \times P_s'(*, t+1, \Delta M[\text{nret}]_{\text{retrieve}}, \\ & \Delta\text{CS}[\text{nret}]_{\text{retrieve}}) \end{aligned} \tag{7}$$

$$P_s(\text{rest}, t, Mass, CS) = SR_{rest} \times P_s'(*, t+1, \Delta M_{rest}, \Delta CS_{rest}) \tag{8}$$

Future survivorship [$P_s'(*, t+1, \text{Mass}, \text{CS})$] is a function of the expected state at time t+1 resulting from decision D. The change in mass resulting from each alternative decision was calculated as follows:

$\Delta M[\text{nprey}]_{\text{eat}}=\text{Mass}+E\times\text{nprey}-\text{MR}_{\text{eating}}$,

where E is mass gained from a food item and nprey is number of food items found.

- $\Delta M_{\text{cache}}=\text{Mass}–\text{MR}_{\text{caching}}$
- $\Delta M[\text{nret}]_{\text{retrieve}}=\text{Mass}+\gamma_{\text{R}}–\text{MR}_{\text{retrieving}}$

(γ_R is defined in Eq. 3 and is a function of nret: the number of seeds retrieved in a 20-min time interval)

- $\Delta M_{\text{rest}}=\text{Mass}–\text{MR}_{\text{resting}}$
- $\Delta M_{\text{nfe}}=\text{Mass}–\text{MR}_{\text{eating}}$
- $\Delta M_{\text{nfc}}=\text{Mass}–\text{MR}_{\text{caching}}$
- $\Delta M_{\text{nfr}}=\text{Mass}–\text{MR}_{\text{retrieving}}$

The change in cache size resulting from each decision was:

- $\Delta\text{CS}_{\text{eat}}=\Delta\text{CS}_{\text{rest}}=\Delta\text{CS}_{\text{nf}}=\text{CS}\times P_{\text{nocacheloss}}$
- $\Delta\text{CS}[\text{nprey}]_{\text{cache}}=\text{CS}\times P_{\text{nocacheloss}}+\text{nprey}$, where *npreу* is the number of new caches
- $\Delta\text{CS}[\text{nret}]_{\text{retrieve}}=\text{CS}\times P_{\text{nocacheloss}}–\gamma_{\text{R}}/\text{M}_{\text{ret}}$

There are three relevant parameters that describe resource dynamics:

- $P_{\text{nocacheloss}}$ is a probability that caches survive one time interval; for all simulations $P_{\text{nocacheloss}}$= 0.9995188 per 20 min, which corresponds to a 20-day cache half-life.

- P_{find} is a probability of finding food.
- $P_{\text{findcaches}}$ is a probability of finding previously made caches.

Finally, SR is a probability of survival (in a single time interval) associated with each behavior and consists of a probability of surviving predation (F_{p}=1-P_{kill}; Eq. 2) and a probability of surviving starvation (1–F_{s}) (note: F_{s} is described above). In our model, we assumed that $\text{SR}_{\text{eat}}=\text{SR}_{\text{cache}}=\text{SR}_{\text{retrieve}}=F_{\text{p}}\times(1-F_{\text{s}})$. Because we assumed that there is no predation risk while resting, $\text{SR}_{\text{rest}}=(1-F_{\text{s}})$.

Night was treated as a 17-h interval with deterministic mass loss and no risk of predation. We assumed that nocturnal mass loss was equal to the basal metabolic rate (MR). Thus a bird starting at Mass=*m* at the end of a day will lose mass overnight equal to MR×17×3 (i.e., 17×3, 20-min time intervals). For each 20-min interval throughout the night, the probability of surviving starvation ($\text{SR}_{\text{starv}}[m]$) at any given Mass=*m* was approximated using an incomplete beta function (described above).

$$P_s(\text{overnight}, T, \text{Mass}, \text{CS}) = P_s{}'(*, t = 1, \text{Mass} - \Delta M_{\text{overnight}}, \text{CS}_{\text{overnight}}) \times \prod_{i=1}^{51} \text{SR}_{\text{starv}} [m - (i \times \text{MR})] \tag{9}$$

Thus the survival rate at the end of the day (time=*T*), with mass=*Mass* and cache size=CS, is the product of the probability of surviving the night (the second half of this equation) and the probability of surviving from the first interval through the rest of the season starting at time *t*=1 the next morning.

$\Delta\text{M}_{\text{overnight}}=\text{MR}\times\Delta t_{\text{night}}$ where Δt_{night} is the number of 20-min time intervals during the night.

$CS_{\text{overnight}}=\text{CS} \times P_{\text{nocacheloss}}\Delta t_{\text{night}}$

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