Behavioral Ecology Vol. 12 No. 2: 246–260

A reevaluation of the logic of pilferage effects, predation risk, and environmental variability on avian energy regulation: the critical role of time budgets

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We studied the effect of pilferage rates, variation in food encounter rate, and predation risk on cache and fat-storage regulation using dynamic programming. Previous predictions that small birds facing increased pilferage rates should cache less and store more body fat are not generally supported. Instead, cache investment (caching rate or percent of food cached) is predicted to be unimodal, peaking at intermediate pilferage rates. This pattern is determined, in part, by pilferage-induced changes in time budgets: at low pilferage rates, a marginal increase in pilferage rates can be offset by an increase in cache investment. However, increased caching increases time allocated to both caching and foraging. The increased foraging is caused by the energetic costs of caching and by the loss of energy from the cache. Increased time spent caching and foraging in turn decreases time spent resting under low predation risk. Above some threshold pilferage rate, the marginal value of resting exceeds the marginal value of caching, and cache investment declines with further increasing pilferage rates. These patterns hold for three levels of variation in food encounter rate: time-invariant, between-day, and within-day variation; they also hold across different mean rates of food encounter. We show that previous predictions concerning decreased energy-storage levels with increased food abundance are not supported when there is between-day variation in mean food encounter rates and food abundance increases only on ''good'' days. Finally, predation risk affects the predictions described above in two ways. First, these trends assume that the birds can rest in a predator-free refuge. If the refuge is not available, birds are predicted to cache less at higher pilferage rates irrespective of the absolute level of pilferage. With the refuge in place, levels of predation risk affect the skew in the pilferage-rate/caching function. As a result, the relative effect of predation risk on caching intensity varies with pilfer rate. At very low pilfer rates, lowered predation risk causes more caching, but lowered predation risk under high pilferage rates can lower caching intensity, contrary to previous predictions. Surprisingly, predation risk has an appreciable effect on body mass only when the bird is predicted to cease caching (i.e., at the highest pilfer rates); otherwise a change of two orders of magnitude in the probability of encountering predators has little effect on body mass. Our results suggest that the tradeoffs associated with the joint regulation of internal energy stores and externally cached stores are more complicated than previous literature would indicate. Our results also show that we have underestimated the role that time budgets play in patterns of energy regulation.
Key words: dynamic optimization, dynamic programming, caching, chickadee, energy regulation, fat regulation, paridae, parus, pilferage, predation risk, poecile, time budgets. *[Behav Ecol 12:246–260 (2001)]*

The study of the adaptive significance of foraging behavior has focused on the diversity of trade-offs associated with behavioral alternatives (Stephens and Krebs, 1986). One critical tradeoff made by foragers who themselves are subject to predation is the balance between starvation risk and predation risk. This is because a reduction in starvation risk generally requires increased levels of energy storage (Pravosudov and Grubb, 1997a; Witter and Cuthill, 1993). However, increased levels of energy storage can increase metabolic expenditures and thereby increase the time required for foraging, a behavior considered to put the animal at enhanced risk of predation (Lima, 1986; McNamara and Houston, 1990). Also, the extra mass associated with fat storage may itself reduce the ability of the forager to avoid predators (Ekman and Hake, 1990; Lima, 1986), although the validity of this cost has received equivocal support (as discussed in the Model section below).

These tradeoffs are complicated further by the fact that animals can store energy in several forms. For example, many animals cache food externally in addition to storing energy internally as fat (Vander Wall, 1990). One fundamental tradeoff faced by animals that cache is the allocation of time and energy to cache maintenance versus internal fat storage. Indeed, cached food and fat are widely seen as substitutable forms of energy storage (Brodin and Clark, 1997; Ekman and Lilliendahl, 1993; Hurly, 1992; Källander and Smith, 1990; Lucas, 1994; Lucas and Walter, 1991; McNamara et al., 1990; see Pravosudov and Grubb, 1997b, 1998, for an alternative view). However, while cached food and fat are both forms of stored energy, there are a number of important differences that may affect the degree to which either form is preferred. There is a fairly strict limit on how much fat an animal can store (Blem and Pagels, 1984), although an advantage to fat storage is that there is little variation in the animal's estimate of the size of the fat reserves. There are also additional factors that limit the value of carrying extra mass, such as increased metabolic rates and increased flight costs (Lima, 1986; Lucas and Walter, 1991; Witter and Cuthill, 1993). In contrast, the size of a bird's

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Received 2 December 1999; revised 12 June 2000; accepted 11 September 2000.

cache is not nearly as constrained as fat stores (Vander Wall, 1990). However, cached food represents a less certain source of energy due to pilferage and the potential for forgotten cache locations (Lucas and Zielinski, 1998). Additional costs unique to the use of cached food as a storage mechanism are the time and energy required to store then retrieve food, and pilferage and memory constraints that can limit the length of time the food can profitably be stored.

A logical extension of the concept of a tradeoff between cache and fat stores is that a reduction in the value of caches, such as through increased cache pilferage, should cause a reduction in caching rates and a concomitant increase in fat reserves (Ekman and Lilliendahl, 1993; Lucas and Walter, 1991; McNamara et al., 1990; Sherry, 1985). We will refer to this idea as the ''prevailing prediction.''

From a practical perspective, cache pilferage is an important component of energy regulation tactics, because it provides a means by which the value of energy storage can easily be manipulated. For example, a cacher's response to experimentally induced cache pilferage can provide a critical insight into the degree to which animals regulate energy stores (Lucas and Zielinski, 1998). However, the only current test of the prevailing prediction generated contradictory results: Carolina chickadees (*Poecile carolinensis*) cached more seeds and cached a higher percentage of encountered seeds when cached seeds were pilfered, compared to conditions in which cached seeds were left in place (Lucas and Zielinski, 1998). Lucas and Zielinski (1998) suggested that these results imply that the general theoretical approach to cache/fat tradeoffs may need to be reevaluated (also see Pravosudov and Grubb, 1998). However, there are alternative explanations for this failure of the prevailing hypothesis. One is that the birds' response to cache pilferage was an artifact of extreme environmental conditions presented in the aviaries (Lucas and Zielinski, 1998). Another possibility is that previous models incorporated appropriate tradeoffs between the maintenance of a cache or fat stores (e.g. Brodin and Clark, 1997; Hurly, 1992; Lucas and Walter, 1991; McNamara et al., 1990), but the effect of pilferage was not fully explored. For example, Lucas and Walter (1991) described the theoretical effect of cache pilferage on cache size and body mass, but not the effect of pilferage on caching behavior (e.g., percent of seeds cached or caching rate). To explore this second alternative, we analyzed an updated version of previous dynamic programs (Brodin, 2000; Lucas and Walter, 1991; McNamara et al., 1990). Here we specifically ask whether the predicted negative correlation between cache intensity and pilferage rate is robust in the context of the ''standard'' approach to the dynamic regulation of energy stores described in these papers. In effect, we ask whether the general theoretical approach taken by previous modelers really does need to be reevaluated, as implied in Lucas and Zielinski (1998).

Three of the most important environmental conditions that should affect regulation of energy storage of any form are variability in the access to food, the level of predation risk, and the mean amount of food available (e.g., McNamara and Houston, 1990). Our analysis of pilferage effects on energy regulation (both fat and cache stores) will incorporate all three conditions.

Many papers focus on the effect of variability in food access on energy regulation (e.g., Kacelnik and Bateson, 1996; McNamara and Houston, 1992). One of the most important advantages of energy storage is that it provides an energy source when foraging is dangerous or food is otherwise difficult to find (Pond, 1978). The presence of predators imposes an obvious immediate mortality risk of foraging, but in addition may reduce the frequency and duration of foraging bouts (Lucas, 1985). Indeed, resources themselves vary over different time scales, from within days to between seasons (Vander Wall, 1990). The scale over which resources vary is a potentially critical component of the ability of an animal to use energy storage to adapt to variation in resource variability (Lucas et al., 1993). Obviously a response to short-term variation in resource abundance (e.g., variation in the rate at which prey are found in a patch) requires very different energy storage strategies than the response to a weather-induced reduction in food availability over the course of days. Nonetheless, much of the literature on energy regulation uses only a single time scale. Here we consider three different environments that vary in the scale of resource variation: one in which mean food encounter rates are constant throughout the day and all days are uniform, a second in which mean food encounter rates vary between days, and a third where food encounter rates vary within days (as might happen in response to interruptions). The effect of pilferage rate on energy regulation is evaluated for each of these environments. We also vary the effect of mean food encounter rates for the first two environments and the effect of the transition probabilities from high to low food encounter rates when resources vary within days. These manipulations allow us to determine how animals should simultaneously manage internal fat reserves and cached food under a variety of foraging conditions.

THE MODEL

We model caching and mass regulation in a small passerine in response to different levels of pilferage, food availability, and predation risk, under temperate zone, winter conditions. The model is an extension of several previous models. We use a more realistic description of cache dynamics than found in McNamara et al. (1990), who assumed that all cached food could be retrieved in any given 30 min period during the day, and that all cached food was pilfered overnight. We use a more realistic description of food encounter rate than found in Lucas and Walter (1991) who assumed that constant food encounter rates occurred over fixed intervals every 2 h during the day, with no food available at other times. We extend McNamara et al.'s (1994) results on foraging interruptions in a non-caching bird to evaluate effects of interruptions (or more generally, within-day variation in access to resources) on a caching bird. We extend a model by Pravosudov and Lucas (in press) who considered only a single, short-term level of variation in food encounter rate. Here we consider two additional temporal scales of variation in access to food: within-day variance (e.g., that might result from short-term interruptions in foraging) and between-day variation (that might result from weather-induced reduction in food access). We extend Brodin's (2000) study of short-term caching. Brodin treated short-term prey encounter rates as fixed (non-stochastic) but allowed for variation in encounter rates from morning to midday to evening. Here we consider a broader range of temporal scales over which food encounter rates might vary. Finally, our model provides a more synoptic view of pilferage effects than found in any of these previous papers.

Brodin and Clark (1997) also modeled between-day variation in food encounter rates, in addition to fall/winter variation (the latter is not addressed with our model). However, their approach differs substantially from ours. They assume that caches whose location the forager forgets are nevertheless available to the forager and that these forgotten items increase the local encounter rate of food (also see Smulders, 1998). In contrast, we assume that forgotten caches are lost and have no effect on subsequent food encounter rates. The two approaches address different life-histories. Ours is likely to be more appropriate for short-term cachers: birds that occupy low-latitudes or high-latitude, winter-caching birds that cache relatively little food. These birds are unlikely to find cached food by chance. Long-term hoarding models are likely to be more appropriate for fall caching of high-latitude species that can cache more than 10,000 seeds in a single season (Brodin, 1994; Pravosudov, 1985). Our model is also designed to evaluate temporal trends on a finer scale than in the Brodin and Clark (1997) model.

We equate cache loss with pilferage throughout the paper, but pilferage is only one of two sources of cache loss. The other is the forgetting of cache locations. Both sources of loss may be functionally equivalent if a bird attempted to retrieve a cache but failed because the item was no longer present or because the cache location was misjudged. Alternatively, if the bird's memory loss results in its never attempting to retrieve the item, then the energetic consequences of pilferage and forgetting would differ. The fine details of cache retrieval are not understood well enough for us to provide a realistic distinction between these alternative sources of cache loss (Lucas and Zielinski, 1998). Therefore, we will assume that "cache loss" is governed by a single process analogous to cache pilferage. Our model addresses how birds should respond to differences in cache-loss rates across different habitats that vary in pilferage rates as well as in the overall probability of finding food. As such, our results appropriately reflect the effect of pilferage rates on energy regulation.

The model is a stochastic dynamic program (Mangel and Clark, 1988), in which body mass and cache size are treated as state variables. We assume that the bird chooses among four alternative behaviors (search for food and eat, search for food and cache, retrieve cached food, or rest) and that the behavior chosen will maximize the probability of over-winter survival. Survival is affected by two sources of mortality, starvation and predation risk.

As with any dynamic program, we divide state and time into discrete intervals. We assumed that day length was 7 h (i.e., day length of Stockholm, Sweden, in late November or Edinburgh, Scotland, in late December). Each 7-h day is divided into 20-min intervals (shortening this to 10 min has no effect on the results). The maximum cache size is 300 food items (increasing this to 400 has no effect on the results), and body mass is assumed to range from 8–12 g divided into 100 increments (increasing this to 150 increments has no effect). This variation in body mass is assumed to be primarily due to changes in internal fat reserves (Blem, 1990). Linear interpolation was used to estimate survival consequences of fractional increments of both body mass and cache size. "Night" was treated as a single 17-hour time interval. Cache pilferage rates were constant throughout a 24-hour day, assuming that caches are susceptible to diurnal and nocturnal seed predators. We ran each dynamic program for the higher of 65 days or twice the cache half-life (i.e., time until there is a 50% chance of a cached seed being lost); our simulations indicate that this amount of time ensures that the data we are describing represent equilibrium conditions.

Mass changes and concomitant changes in starvation risk are a function of the behavior-dependent metabolic rates, food encounter rates, and the longevity of cached food items. Each of these elements is discussed below, followed by a description of predation risk.

Metabolic rate

Mass-dependent metabolic rates were taken from Lucas and Walter (1991) and scaled for 20-minute intervals. Basal metabolism was:

$$BMR = 0.00616 \cdot T \cdot (mass/1000)^{0.66}$$

where

$BMR =$ basal metabolic rate measured in g mass lost per 20 min,

$T = 45.7 - 1.33 \cdot temperature,$

$temperature = -5°\mathrm{C}$ for all simulations

$mass =$ body mass measured in g

The metabolic rate of the four alternative behaviors and nighttime rate was taken as multiples of *BMR*:

$$MR_{\mathrm{cache}} = 8.0BMR \qquad MR_{\mathrm{eat}} = 8.0BMR$$

$$MR_{\mathrm{retrieve}} = 8.0BMR \qquad MR_{\mathrm{rest}} = 1.95BMR$$

$$MR_{\mathrm{night}} = 1.0BMR$$

The value for resting metabolic rate is from Buttemer et al. (1986). The values for active foraging (cache, eat, or retrieve) are based on the fact that short flights (which are typical of the mode of foraging in the Paridae) cost 12 × nighttime *BMR* (Carlson and Moreno, 1992). Thus, we assume the cost of active foraging is intermediate between the costs of rest and short flight.

Food encounter rate

Three behaviors result in the encounter of food items: retrieval, searching and eating encountered food, and searching and caching encountered food. We assume that the number of food items encountered per 20 min when engaged in any of these behaviors can be described using a truncated normal probability distribution. The approximations of food encounter rates we used are derived from data on small parids in Pravosudov (1983, 1985) and Brodin (1994), converted to fat equivalents using estimates from Lucas and Walter (1991). We also assume that food encounter rates are independent of the frequency of caching exhibited by other birds (see Smulders, 1998, for an alternative approach).

Retrieval

We assume that food encounter rate while retrieving increases with the number of food items in the cache. The rationale is that a higher density of caches allows for a shorter mean distance that a bird will have to fly to the nearest cache site, and therefore a more rapid retrieval of those caches compared to a condition with a lower cache density. We also assume that retrieval encounter rate is not affected by the abundance of uncached food. Thus, encounter rate while retrieving (γ_R), measured in g mass gained/20 min, was:

$$\gamma'_R = 0.26 \times (1.0 + 0.2 \times (1 - e^{-0.025 \times CS})) \pm 0.04 \qquad (1)$$

$$\gamma_R = \min(\gamma'_R, 0.04 \times CS) \qquad (2)$$

where $CS =$ cache size.

The interpretation of Equation 1 is as follows: The birds retrieve a baseline of 0.26 ± 0.04 g/20 min. As cache size increases, the actual encounter rate asymptotes at 0.31 ± 0.04 g (i.e., 1.2 × 0.26). Equation 2 states that retrieval rate is constrained to be no more than the body fat derived from all the food currently in the bird's cache (each item represents a gain of 0.04 g fat).

Search

We assume that mean food encounter rates while searching are fixed irrespective of whether the birds ultimately cache or eat the food. We simulated three types of environments, each of which is characterized by a different level of variability in food encounter rate.

Table 1

Patch transition probabilities for within-day variance environments

Previous interval	Current interval Low quality	 High quality
Low quality	P_{LL}	$P_{LH} = 1 - P_{LL}$
High quality	$P_{HL} = 1 - P_{HH}$	P_{HH}

(1) Search—time-invariant variance

In this type of environment we assume that the mean encounter rate and its variance are fixed both within and across days. We simulated three different time-invariant-variance environments by testing three mean search encounter rates (0.17, 0.19, and 0.21 g/20 min). The standard deviation in search encounter rate was 0.08 for all simulations. Note in all cases that mean search encounter rates are lower than mean retrieval encounter rates and that the variance in encounter rates is higher for search than for retrieval.

(2) Search—between-day variance

In this environment type, we assume that there are two types of day, good and bad. This would simulate, for example, weather patterns that limit a bird's capacity to locate noncached food on ''bad'' days. The days differ in food encounter rate while searching (as opposed to retrieving caches). Mean encounter rate within each day type is assumed to be constant. We assume that the arrival of good and bad days is a Markov process in which the probability that any given day is good is $P_G = .9$ (thus the probability of a bad day is $P_B = .1$.) We ran three simulated environments that varied in food encounter rate on good days (0.17, 0.19, and 0.22 g/20 min) with a fixed encounter rate on bad days (0.12 g/20 min). We also ran three simulated environments that varied in food encounter rate on bad days (0.12, 0.15, and 0.17 g/20 min) with a fixed encounter rate on good days (0.22 g/20 min). The standard deviation of the encounter rates was 0.08 for all environments and both day types.

(3) Search—within-day variance

In this environment, we assume that all days are the same. However, there is a fixed probability that prey encounter rates vary between two levels (high and low) from one time interval to the next. Conceptually, this within-day variation could be viewed as stochastic variation in food-patch quality (note: here patches do not deplete), or it could be viewed as an interruption of foraging activity (e.g., by a dominant bird or by a predator) that restricts access to food in a homogeneous environment. If the bird is in a poor-quality patch (or is interrupted), search encounter rates (γ_{SL}) are approximately one half of the search encounter rates when the bird is in a high-quality patch (or is not interrupted) (γ_{SH}):

$$\gamma_{SH} = 0.22 \pm 0.08 \text{ g/20 min} \qquad \gamma_{SL} = 0.10 \pm 0.08 \text{ g/20 min}$$

We assume that access to cached food is unaffected by this variation in prey encounter rates. We model the transition between patch types with a 2 × 2 transition matrix that describes the probability of being in a patch of either type in any 20-min interval given that the bird was in either patch type in the last 20-min interval (Table 1). We simulated two different environments for these conditions:

$$I_1 = (P_{LL1} = 0.4,\ P_{HH1} = 0.8)$$

$$I_2 = (P_{LL2} = 0.2,\ P_{HH2} = 0.9)$$

Thus, for example in environment I_1, if the forager is in a low-quality patch in a previous interval then there is a 40% chance that it will stay in a low-quality patch in the current interval ($P_{LL} = .4$). There is also an 80% chance that a forager in a high-quality patch in the previous interval stays in that patch in the current interval ($P_{HH} = .8$).

In the first interruption environment, (I_1), the average duration of a block of continuously uninterrupted foraging is 100 min, and the average duration of a block of continuously interrupted foraging is 33 min (note: the minimum duration in our model is 20 min, the length of a single time interval). In the second interruption environment, (I_2), the average duration of a block of uninterrupted foraging is 200 min, and the average duration of a block of interrupted foraging is 25 min. Heuristically, if patch quality results from interruptions then longer interruptions in environment I_1 could be caused by the arrival of a top predator (e.g., sharp-shinned hawk, *Accipter striatus*), whereas shorter interruptions in I_2 could be caused by the arrival of a dominant conspecific. If patch quality is caused by variation in prey abundance, then environment I_1 would have larger (or more) low-quality patches and smaller (or fewer) high-quality patches than environment I_2.

Cache loss (pilferage)

We model pilferage as a fractional loss of the cache in each 20-min interval. For any given simulation, pilferage rates are treated as constant (i.e., with neither between-day nor within-day variation). We varied pilferage rates (range: 0.86 to 100.00 percent lost per day) to test for the effect of pilferage rate on energy regulation patterns. Pilferage rates are described as the percent of items lost per day, although pilferage loss was imposed in each 20-min interval throughout the day.

Starvation risk

We have described the mass-dependent metabolic loss and the environment-dependent increase in mass that results from retrieving or searching for food items. The net change in mass resulting from these two processes affects survival through mass-dependent starvation risk. Following Lucas and Walter (1991), we assume that the risk of starvation for birds above 8.4 g is zero. An incomplete beta function was used to model the starvation risk for birds ranging from 8 g ($P_{\text{starve}} = 1.0$) to 8.4 g ($P_{\text{starve}} = .0$). 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 $0 \leq x \leq 1$. The arguments (a,b) determine the relative shape of the curve. In our simulations, $a = b = 3.3$, as in Lucas and Walter (1991). Thus:

$$p_{\text{starve}} = \begin{cases} 0 & mass \geq 8.4 \text{ g} \\ I_x(3.3,\ 3.3) & 8.0 \leq mass < 8.4 \text{ g} \end{cases}$$

where $x = (mass - 8)/0.4$

Predation risk

Following Lima (1986) and Lucas and Walter (1991), we modeled predation as a two-step process, including the probability that a predator is encountered in a given 20-min interval ($P_{\text{encounter}}$) and the probability that the bird is killed conditional upon encounter ($P_{\text{kill|encounter}}$). For our baseline condition, we assume that the bird is not at risk of predation ($P_{\text{encounter}} = 0$) while resting or while roosting overnight, and that predation risk while retrieving or searching for food (i.e., foraging) is $P_{\text{encounter}} = 0.67 \times 10^{-3}$. This latter figure is in the middle of the range used in Lucas and Walter (1991). We evaluate the effect of levels of predation risk on energy regulation tactics by varying $P_{encounter}$. Three alternative conditions

Table 2
Synopsis of predictions for each of the three simulated environments

	Environment		
Variables	Time-invariant variance	Between-day variance	Within-day variance
1. Pilferage rate	a. Cache size declines with increased pilf. rate	a. Same as time-invariant variance	a. Same as time-invariant variance
	b. Body mass increases with increased pilf. rate	b. Same as time-invariant variance	b. Same as time-invariant variance
	c. % food cached is a unimodal function of pilf. rate (assumes there is a predator-safe refuge)	c. Same as time-invariant variance	c. Same as time-invariant variance
2. Time budgets	a. *Over a range of low pilf. rates:* eating & caching increase, resting decreases with increased pilf. rates	a. Same as time-invariant variance	a. Same as time-invariant variance
	b. *Over a range of high pilf. rates:* eating & caching decrease, resting increases with increased pilf. rates	b. Same as time-invariant variance	b. Same as time-invariant variance
			c. Birds tend to rest in low-quality patches when encounter rates are low
3. Predation risk	a. *No refuge (i.e., pred risk same when foraging or resting):* % food cached declines and mass increases with increased pilf. rates	a. *No refuge:* Same as time-invariant variance	a. *No refuge:* Same as time-invariant variance
	b. *With refuge (no pred risk while resting):* —% food cached declines with increased pred. risk —little effect of pred. risk on body mass unless high pilferage rates eliminate caching	b. *Refuge:* Same as time-invariant variance except overall higher caching intensity —eating replaces resting at low predator risk; resting instead of eating at high pred. risk	b. *Refuge:* Same as time-invariant variance except overall higher caching intensity —caching/pred risk correlation does not hold with the combination of high pilf. rates and low predator risk (here eating is preferred to caching)
4. Food encounter rate	Increased food encounter rate decreases % food cached at low pilf. rates and decreases body mass at high pilf. rates (when caching ceases)	Increased food encounter rate *decreases* % food cached on good days and *increases* % food cached on bad days	

are considered. For two of these we increase or decrease foraging $P_{encounter}$ by an order of magnitude compared to the baseline condition (0.67×10^{-2} and 0.67×10^{-4}, respectively). For the third condition, we let the predation risk while resting be equivalent to the baseline predation risk while foraging, in effect eliminating any predator-safe refuge.

Lima (1986) and Lucas and Walter (1991) modeled the conditional capture probability as a quadratic function of body mass; however, over the range of body mass we are simulating, the quadratic function is nearly linear. Current empirical evidence (Kullberg, 1998) indicates that the escape response is not mass dependent for birds carrying low to moderate fat loads, although birds with very high fat loads may suffer increased predation risk (also see van der Veen and Lindstrom, 2000). Thus escape probabilities are likely to be an accelerating (non-linear) function of mass. We therefore chose an arbitrary function with predation-risk values similar to those of Lima's (1986) model at the extreme mass values in our model ($P_{\text{kill|encounter}} = .078$ at mass = 8 g; $P_{\text{kill|encounter}} = .173$ at mass = 12 g), but that also included an accelerating risk with an increase in mass.

$$P_{\text{kill|encounter}} = .078 + (0.5 \times 10^{-8} \times e^{1.4 \times mass})$$

where *mass* is measured in g.

The probability of depredation is:

$$P_{\text{kill}} = P_{\text{encounter}} \times P_{\text{kill|encounter}},$$

and the probability of surviving both depredation and starvation is:

$$P_{\text{survive}} = (1 - P_{\text{starve}}) \times (1 - P_{\text{kill}}).$$

RESULTS

Our model results are described separately for each environment type. In each case, we consider the effect of pilferage on cache size, body mass, percent of food items cached, and time budgets (i.e., the proportion of the day spent resting, eating, caching food, or retrieving food). Table 2 provides a synopsis of the main results.

Time-invariant variance

If the mean and variance of the food encounter rate are constant, cache size is predicted to decline with increasing pilferage rates (Figure 1A). The birds are predicted to increase body mass to compensate for a reduction in cache size, but the compensation does not occur at the highest food density we simulated (0.21 g/20 min in Figure 1B). These results are consistent with the prevailing prediction (see Introduction). However contrary to the prevailing prediction, the percent of encountered food items that are cached is maximal at intermediate (rather than at lowest) pilferage rates (Figure 2A).

The percent of food items cached and caching rate (number of items cached per unit time) are alternative ways of measuring the investment a bird makes in its cache. Both caching rate and percent food items cached are predicted to increase with an increase in pilferage rate until some threshold, and at pilferage rates above this threshold cache invest-

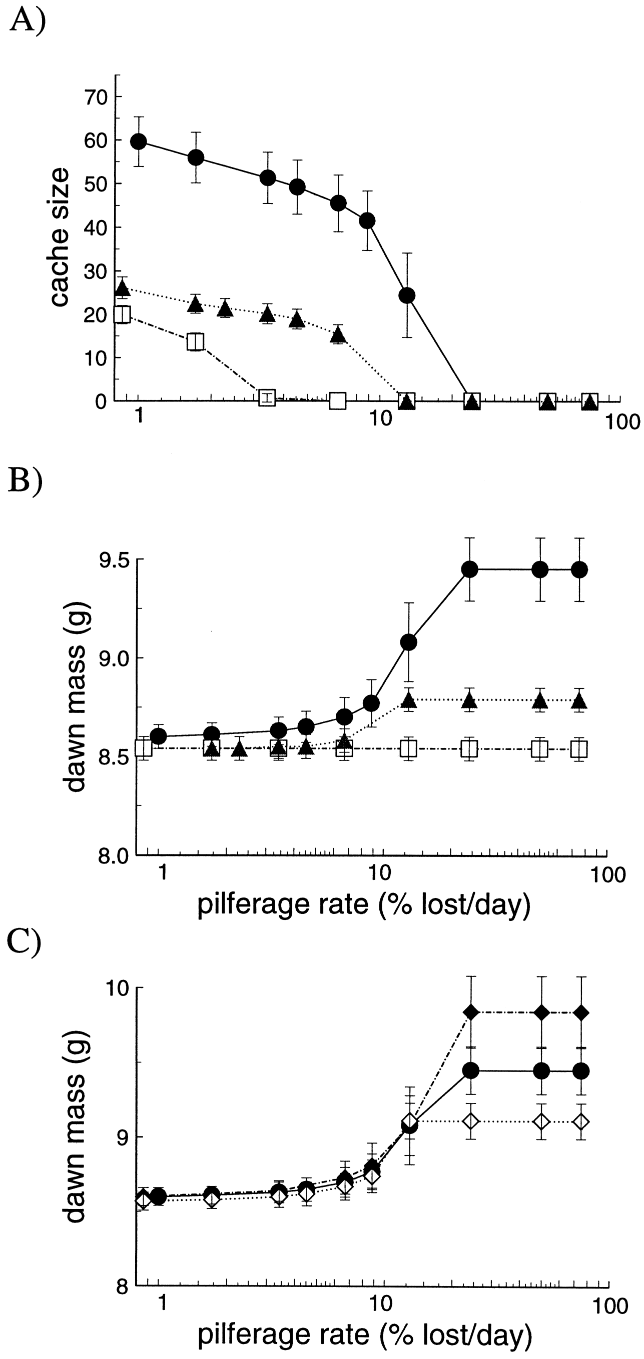

Figure 1
(A) Dusk cache size and (B) dawn mass, both as a function of pilferage rate for three levels of mean food encounter rate; ●: 0.17 g/20 min; ▲: 0.19 g/20 min; □: 0.21 g/20 min. (C) Dawn mass as a function of pilferage rate for three levels of the probability of encountering a predator ($P_{encounter}$): ◆: .00006; ●: .0006; ◇: .006. For (A) and (B), $P_{encounter}$ = .0006. For (C), mean food encounter rate is 0.17 g/20 min. Error bars are SD. derived from a forward simulation of the decision matrix generated by the dynamic program (see text). These relationships are for "time-invariant variance" (see text).

ment then declines sharply with continued increase in pilferage (data not shown). In fact, the percent of food items cached and caching rate exhibit similar patterns for all three environments. To simplify the presentation of our data, we will show only percent cached.

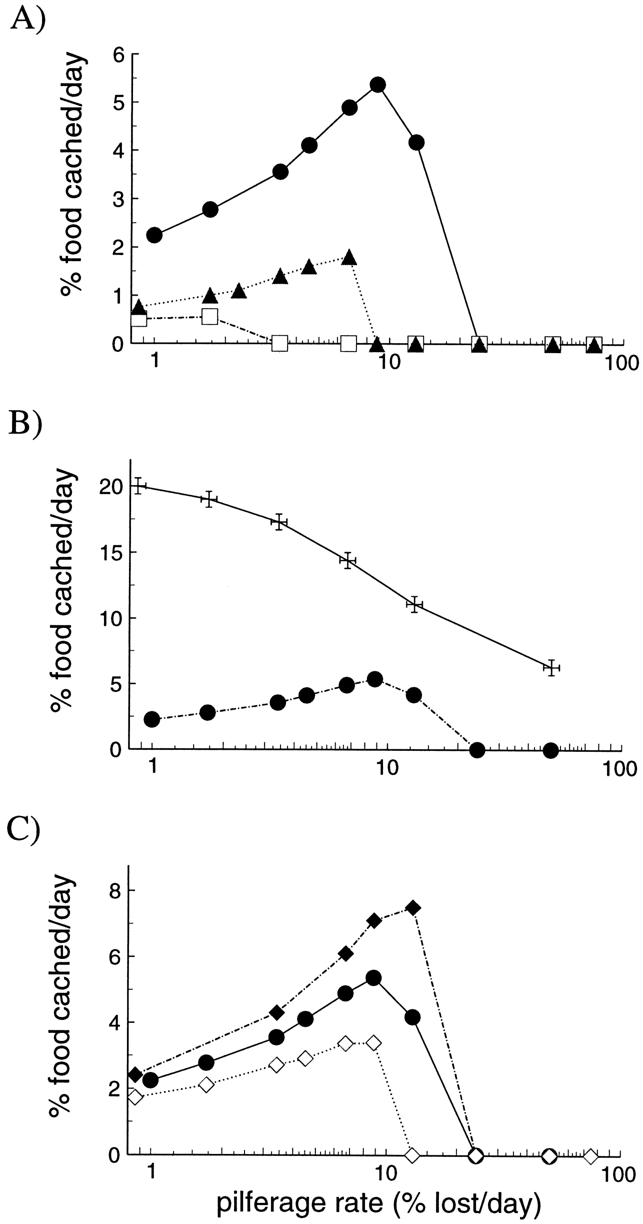

Figure 2
Percent of food cached per day as a function of pilferage rate. These relationships are for 'time-invariant variance' (see text). (A) mean food encounter rate varies from 0.17 g/20 min (●), to 0.19 g/20 min (▲), to 0.21 g/20 min (□). (B) Probability of encountering a predator while resting is .0 (●) or .0006 (cross). Mean food encounter rate is 0.17 g/20 and probability of encountering a predator while foraging is .0006 for both simulations. (C) Probability of encountering a predator while foraging is .00006 (◆), .0006 (●), or .006 (◇). Mean food encounter rate is 0.17 g/20 and probability of encountering a predator while resting is .0 for both simulations.

The unimodal pattern in cache investment (as a function of pilferage rate) can be understood based on the effect of pilferage rate on the time budget (Figure 3). Time budgets were estimated using a forward simulation from the decision matrix generated by the dynamic program (as in McNamara et al., 1990). In essence, the forward simulation calculates the probability that a given forager is engaged in any of the four alternative behaviors at any given time interval throughout the day. These probability distributions are then averaged over

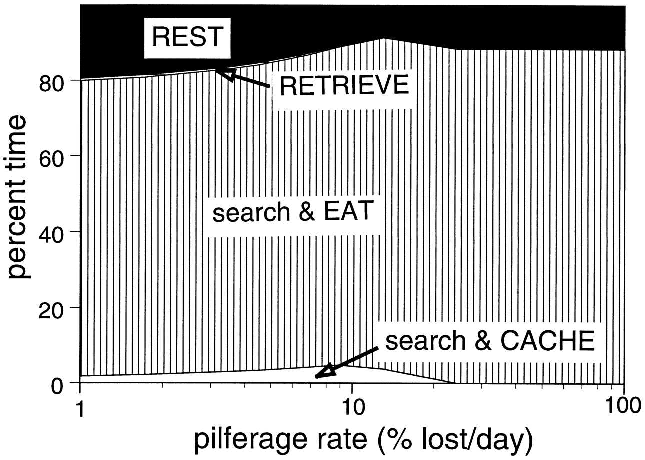

Figure 3
Predicted daily time budget as a function of pilferage rate. Mean food encounter rate is 0.17 g/20 min. These relationships are for "time-invariant variance" (see text). Note that the "retrieve" area is a thin line between "rest" and "search & eat."

the day to get a daily mean proportion of time spent in each behavior. An alternative way of viewing these results is that they represent the mean fraction of a population of birds that would be expected to engage in any of the four behavior patterns over the course of the day.

The results from the forward simulation underscore the fundamental role that time budgets, and explicitly tradeoffs between resting in a predator-safe refuge versus foraging, play in energy regulation. From low to intermediate pilferage rates, the bird increases the time invested in caching to compensate for a loss of cached food. This increased caching incurs an energetic cost, which must be compensated for by a further increase in time spent eating. The increase in metabolic expenditure with increased pilferage rate is exacerbated by an increase in body mass (Figure 1B), which also increases time spent eating. The combination of increased caching and eating time comes at the expense of a reduction in time spent resting in a predator-safe refuge (Figure 3). At some threshold pilferage rate, the marginal value of rest exceeds the marginal value of caching. Beyond this threshold, caching rates decline and eventually drop to zero when pilferage rates are so high that birds simply eat any encountered food.

Predation risk can influence energy regulation patterns in two important ways. First, if there is no predator-safe refuge (i.e., $P_{encounter}$ is the same for resting and foraging), then caching investment declines monotonically with an increase in pilferage rate (Figure 2B). Here, the birds never rest (data not shown), and energy regulation reflects a simple tradeoff between eating and caching. Second, the shape of the percent-cached/pilfer-rate function is relatively unaffected by a change in predation risk incurred while foraging (Figure 2C). Nonetheless, predation risk has a substantial effect on cache regulation: caching increases with a reduction in predation risk at any given fixed level of pilferage rate, and increased predation shifts the peak caching rate to higher pilferage rates (Figure 2C). Surprisingly, predation risk has an appreciable effect on body mass only when the bird is predicted to cease caching (i.e., at the highest pilfer rates); otherwise a change of two orders of magnitude in the probability of encountering predators has little effect on body mass (Figure 1C).

Note that, over the entire range of pilferage rates, the birds are never predicted to overcompensate for pilferage by increasing cache size (Figure 1A). Also, the mean food encounter rate will determine, in part, the shape of the percent-cached/pilferage-rate function. Increased food availability decreases overall caching rates and shifts the maximal point of the function to lower pilferage rates (Figure 2A). Increasing food encounter rate also causes an overall reduction in energy storage: cache size decreases with encounter rate at low pilferage rates (Figure 1A) and body mass decreases with encounter rate at high pilferage rates (Figure 1B).

Between-day variance

For this version of the model, we keep mean and variance in food encounter rates constant within days but allow for variation between days. If we vary food encounter rates on good days and keep the encounter rates on bad days constant, our results are broadly similar to those described above: cache size declines (Figure 4A) and body mass increases (Figure 4B) with increasing pilferage rates, and the percent of food items cached is generally a unimodal function of pilferage rates (Figure 5A; note that there is no caching on bad days). However, the occurrence of "bad" days is expected to cause birds to maintain substantially larger caches relative to environments with constant food encounter rates (compare Figure 4A with Figure 1A).

Similar to the results for time-invariant variance, tradeoffs between resting and foraging are a critical component of the relationship between cache intensity and pilferage rate. On good days with relatively low food encounter rates (0.17 ± 0.08 g/20 min), the percent of time spent resting in a predator-safe refuge is expected to drop to zero when caching rates are at their peak (Figure 6A). Similar results are generated for bad days (Figure 6B). The lack of rest will constrain caching rates, because the bird will be incapable of increasing search (for both cached and eaten food) by reducing time spent resting. However, this constraint is not universally characteristic of between-day variation. For example, with higher mean food encounter rates on good days (0.22 ± 0.08 g/20 min), the birds are able to rest at all pilferage rates (Figure 6C), even on bad days (Figure 6D).

Increased mean food encounter rates on good days induce more caching overall and a shift in the peak of the percent-cache/pilferage-rate function to higher pilferage rates (Figure 5A). Surprisingly, this result is completely opposite to the predicted decrease in caching intensity with increased food encounter rate seen with time-invariant variance. An additional, potentially counterintuitive, result is that increased food encounter rates on bad days induce less caching overall and a shift in the peak to lower pilferage rates (Figure 5B). Thus, changes in food encounter rates on good versus bad days have opposite effects on caching intensities.

Interestingly, tradeoffs associated with time budgets expressed on both good and bad days can also generate a bimodal percent-cached/pilferage-rate function (Figure 5B). On good days, the tradeoff between time invested in resting versus time invested in caching plus eating (see Figure 7A at pilferage rates >4% per day; the tradeoff is also clearly shown in Figure 6C for a different set of parameter values) results in the higher peak in Figure 5B (see the middle function, 0.15 g/20 min encounter rates). The lower peak in Figure 5B results from a different tradeoff between the use of cached food and the use of encountered (and uncached) food, a tradeoff that drives changes in time budgets primarily exhibited on bad days. On bad days, this tradeoff is expressed as a predicted shift from cache retrieval at very low pilferage rates to eating uncached food at somewhat higher pilferage rates (see Figure 7B at pilferage rates <4% per day; also see Figure 6D for a different example). In effect, increased pilferage rates decrease cache size, that in turn forces the bird to search more for uncached food. The former tradeoff (rest versus cache/eat) is a charac-

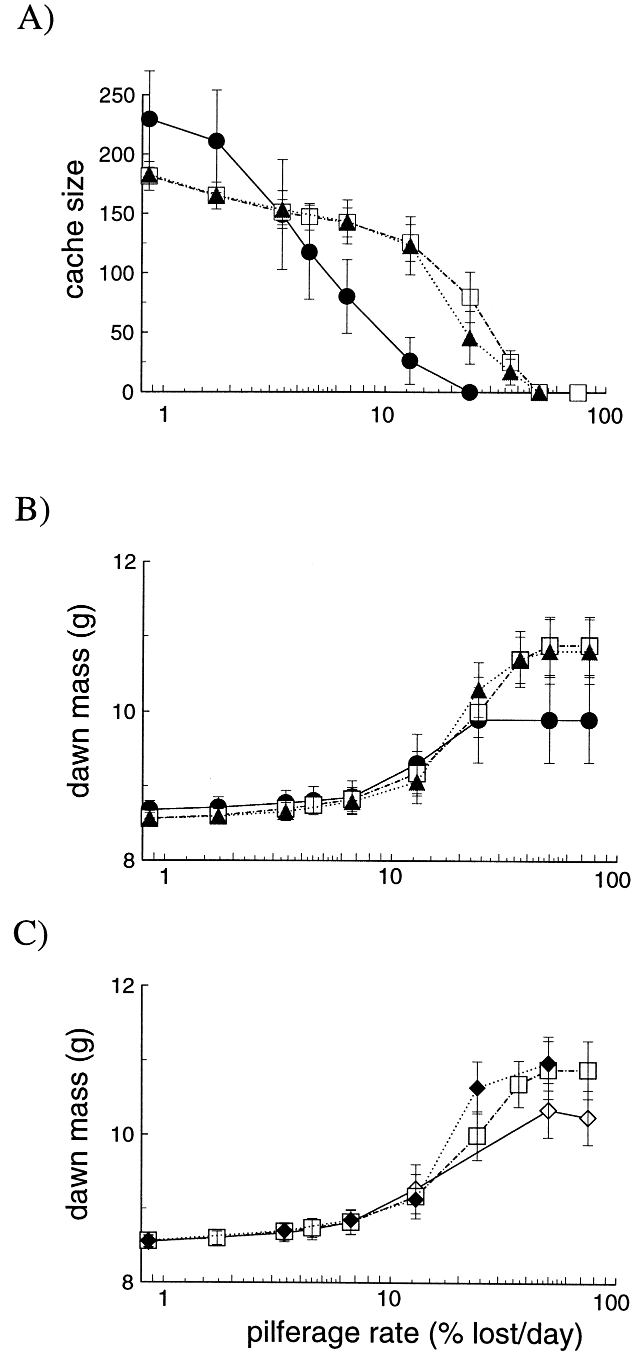

Figure 4
(A) Dusk cache size and (B) dawn mass, both as a function of pilferage rate for three levels of mean food encounter rate. Different symbols represent different food encounter rates on "good" days. ●: 0.17 g/20 min; ▲: 0.19 g/20 min; □: 0.22 g/20 min. (C) Dawn mass as a function of pilferage rate for three levels of the probability of encountering a predator ($P_{encounter}$): ♦: .00006; □: .0006; ◇: .006. For (A) and (B), $P_{encounter}$ = .0006. For (C), food encounter rate was 0.22 g/20 min. Error bars are SD (as in Figure 1). These relationships are for "between-day variance" (see text). Food encounter rate on "bad" days was 0.12 g/20 min for all simulations.

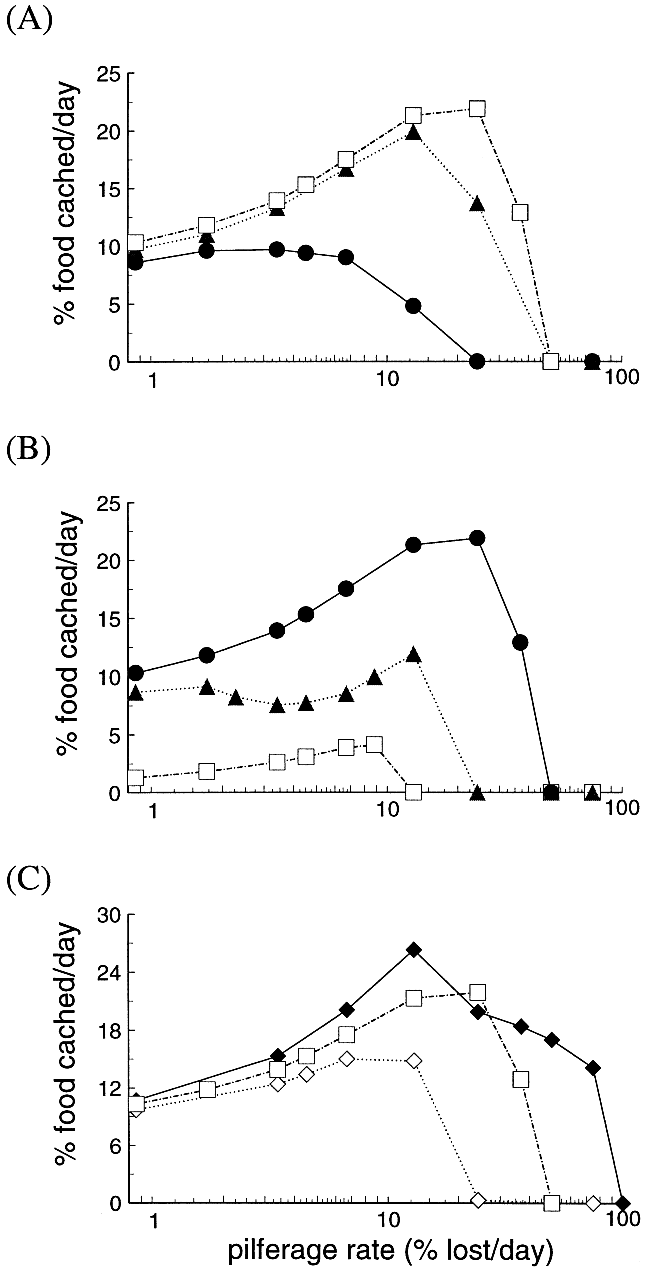

Figure 5
Percent of food cached on "good" days as a function of pilferage rate for between-day variation in food encounter rates (see text). (A) Represents the effect of food encounter rates on "good" days (see Figure 4A for definitions); (B) represents the effect of food encounter rates on "bad" days. ●: 0.12 g/20 min; ▲: 0.15 g/20 min; □: 0.17 g/20 min. Mean food encounter rate on "good" days was 0.22 g/20 min for all three symbols. (C) The effect of predation risk on percent food cached as a function of pilferage rate (see Figure 4C for definitions of symbols). For (A) and (B), $P_{encounter}$ = .0006.

teristic of all simulations we ran. The latter tradeoff is not shown under high food encounter rates on bad days (see Figure 7C,D for time budgets) when the birds rely primarily on locating uncached food items. These tradeoffs also affect total cache size, causing somewhat different shapes in the pilferage-rate/cache-size function (Figure 4A).

If we eliminate the predator-safe refuge (i.e., set $P_{encounter}$ the same for resting and foraging), then the birds never rest (data

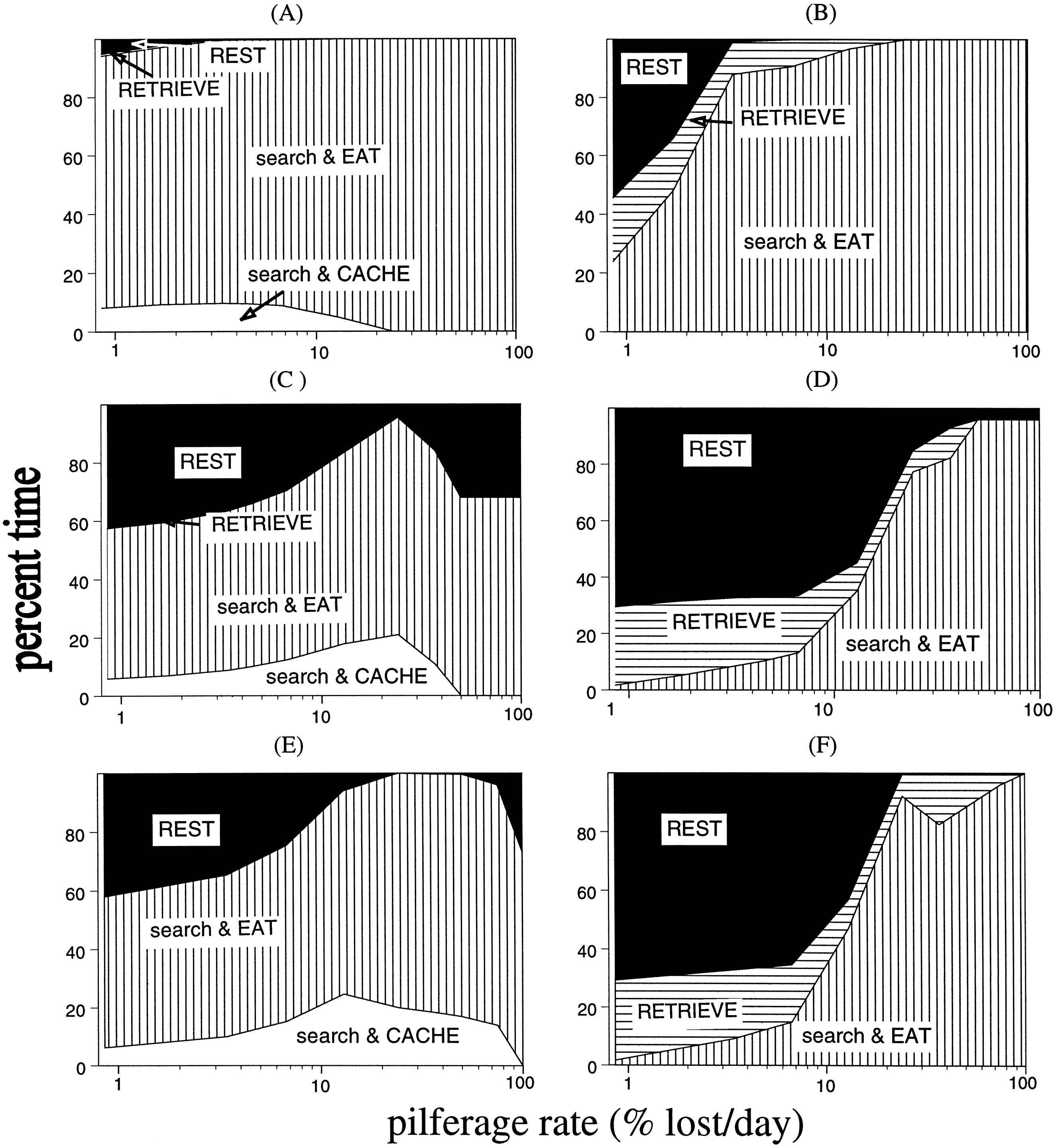

Figure 6

Predicted daily time budget as a function of pilferage rate for between-day variance in food encounter rates (see text). (A)—(D) illustrate the effect on time budgets of mean food encounter rate on "good" days. (C)–(F) illustrate the effect of predation risk on time budgets. Mean food encounter rate on "good" days was 0.17 g/20 min in Figure (A) and (B); food encounter rate on "good" days was 0.22 g/20 min in Figure (C)–(F). Food encounter rate on "bad" days was 0.12 g/20 min for all figures. $P_{encounter}$ (see text) was .0006 for (A)–(D) and .00006 for (E) and (F). (A), (C) and (E) represent time budgets on "good" days; (B), (D) and (F) represent time budgets on "bad" days.

not shown) and cache investment simply decreases with an increase in pilferage (data not shown). This is the same result we found with time-invariant variance (see above) and underscores the relative importance of rest on our results. If the refuge is retained, the birds are generally predicted to increase cache investment with a decrease in predation risk (Figure 5C). This trend is also similar to that reported above for time-invariant variance (Figure 2C), although cache intensity is much higher with between-day variation in resources than with time-invariant variation. However, there is an exception to the cache-investment relationship at moderately high pilferage rates where decreased predation risk actually causes a

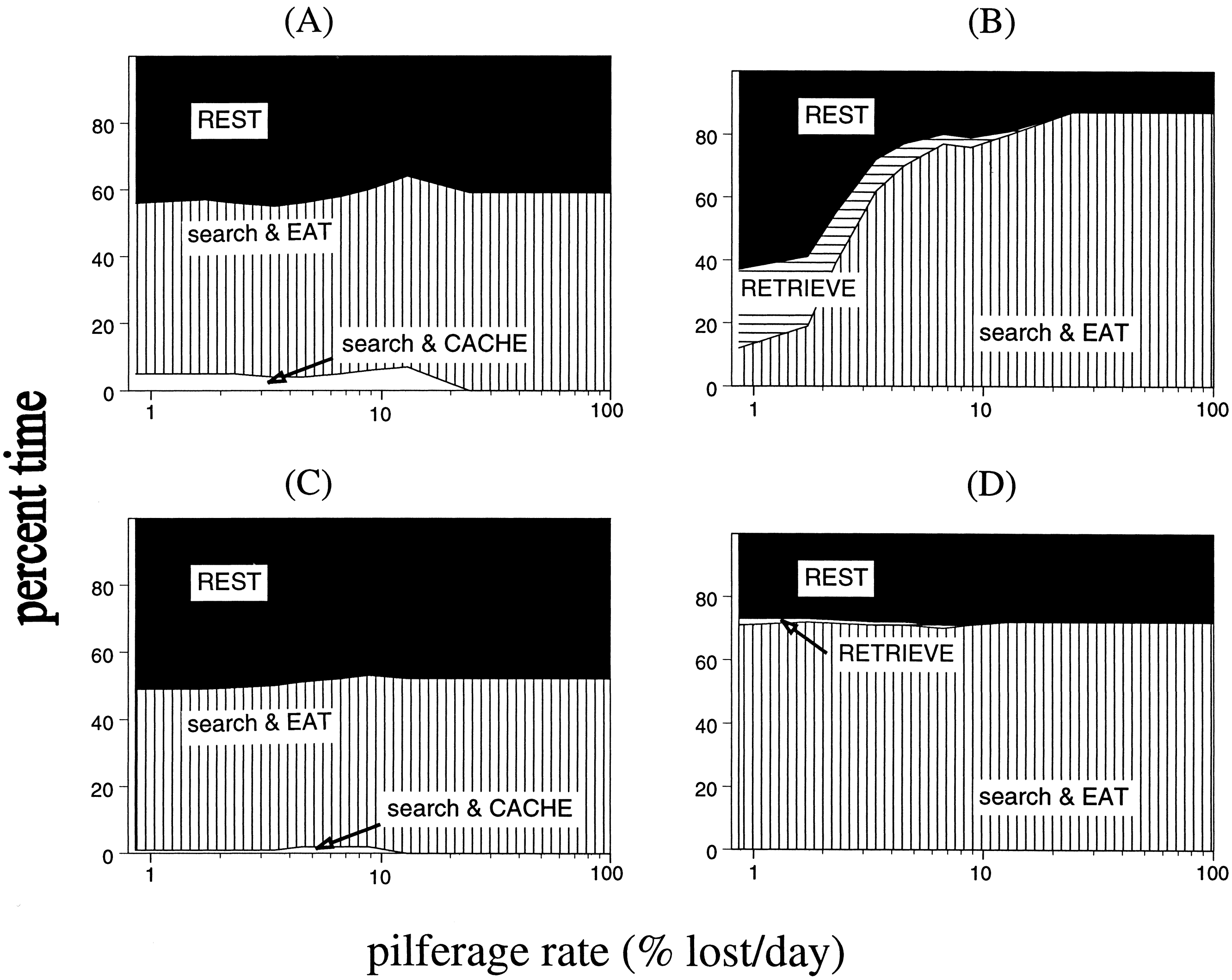

Figure 7
Predicted daily time budget as a function of pilferage rate for between-day variance in food encounter rates (see text). Mean food encounter rate on ‘bad’ days was 0.15 g/20 min in Figure (A) and (B); food encounter rate on "bad" days was 0.17 g/20 min in Figure (C) and (D). Food encounter rate on "good" days was 0.22 g/20 min for all figures. (A) and (C) represent time budgets on "good" days; (B) and (D) represent time budgets on "bad" days.

decrease in cache investment (Figure 5C). We address this exception below where we discuss time budgets.

Caching requires an overall increase in time invested in foraging and an increase in predation risk generally reduces the relative value of foraging compared to resting (Figure 5C). However, consider the effect of pilferage rates on this relationship. As pilferage increases, the birds must compensate for cache pilferage by reducing time spent resting. At moderately high levels of predation risk (here $P_{encounter} = 6 \times 10^{-4}$), there is some level of pilferage above which the bird should reduce caching intensity and instead spend more time at rest in a predator-free refuge (Figure 6C). However, if predation risk while foraging is low enough (here $P_{encounter} = 6 \times 10^{-5}$), then the bird can compensate for cache loss by eating instead of resting on good days (compare Figure 6C and 6E), and foraging (eating and retrieving) instead of resting on bad days (compare Figure 6D and 6F). Thus predation levels have a direct effect on the allocation of time to resting or foraging, and also on the investment in energy storage patterns.

Finally, if the birds cache appreciable amounts of food (i.e., at low pilferage rates; Figure 4A) then mean dawn mass levels are relatively unaffected by changes in either food encounter rates on good days or by changes in the level of predation risk (Figure 4C). This trend is similar to that seen with time-invariant variation (Figure 1C).

Within-day variance

The patterns observed with within-day variation in prey encounter rates are similar to those observed with time-invariant variation and between-day variation: cache size is predicted to generally decline with increases in the pilferage rate (Figure 8A), and the reduction in cache size should be offset by an increase in mass (Figure 8B). In addition, the percent of food cached should increase with an increase in pilferage rate until some threshold pilferage rate, and decline above the threshold (Figure 9A). Similar to the results for environments with between-day resource variation, overall cache sizes are predicted to be larger under conditions of within-day variance compared to conditions of time-invariant variance (compare Figure 1A,B with Figure 8A,B).

For the simulations with time-invariant variation and with

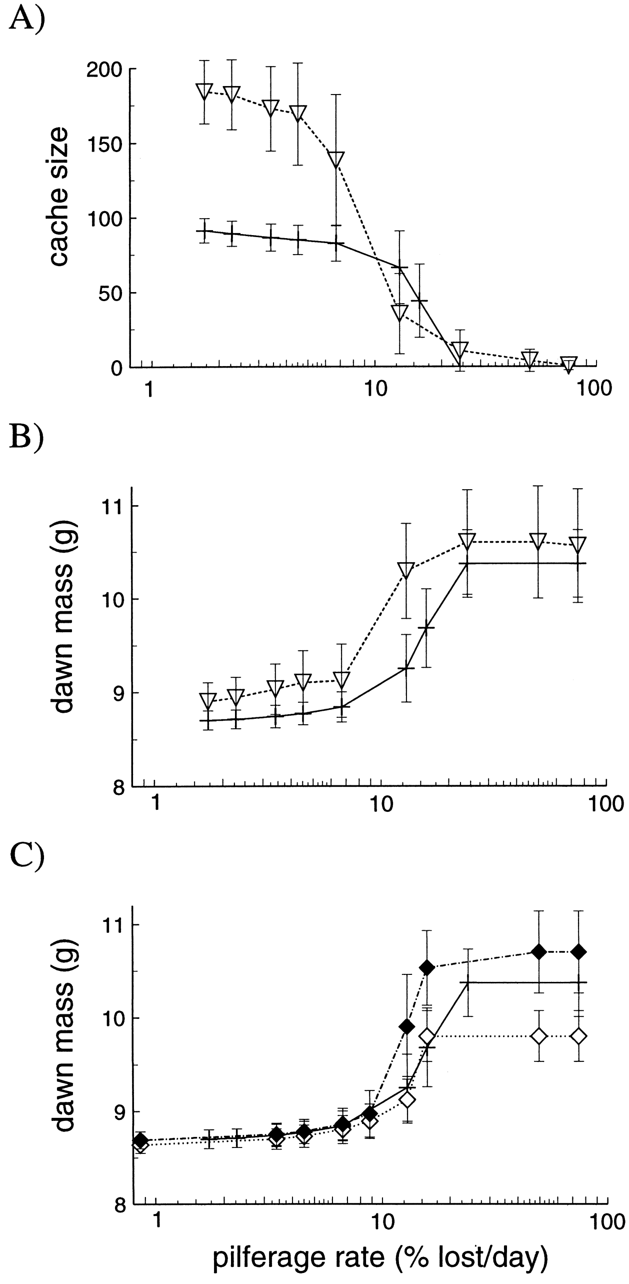

Figure 8
(A) Cache size and (B) dawn mass, both as a function of pilferage rate for two levels of within-day variation in prey encounter rates. $\nabla P_{\mathrm{LL}} = .2$, $P_{\mathrm{HH}} = .9$; +: $P_{\mathrm{LL}} = .4$, $P_{\mathrm{HH}} = .8$. See text for description of environment and for definitions of variables. (C) Dawn mass as a function of pilferage rate for three levels of the probability of encountering a predator ($P_{encounter}$): ♦: .00006; +: .0006; ◊: 0.006. For (A) and (B), $P_{encounter} = .0006$. Error bars are SD (as in Figure 1).

between-day variation, at any fixed pilferage rate the percent of seeds cached per day either decreased (Figure 2 and Figure 5B) or increased (Figure 5A) monotonically with an increase in the level of food availability. Within-day variation does not generate the same pattern. For example, at low and high pilferage rates, short infrequent periods of low food availability (e.g., interruptions) induce a higher percent food cached than longer more frequent periods of low food availability. However, this relationship is reversed at intermediate pilferage rates (Figure 9A).

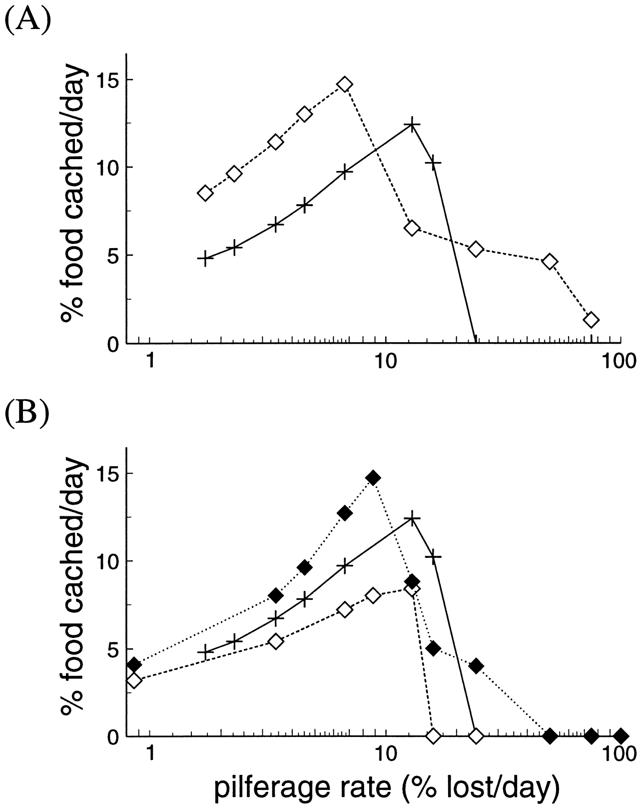

Figure 9
Percent of food cached per day as a function of pilferage rate. These relationships are for environments with within-day variation in prey encounter rates (see text). (A) The effect of two different types of variance on food caching. ◊: $P_{\mathrm{LL}} = .2$, $P_{\mathrm{HH}} = .9$; +: $P_{\mathrm{LL}} = .4$, $P_{\mathrm{HH}} = .8$. (B) The effect of different levels of predation risk on food caching. $P_{encounter}$: ♦: .00006; +: .0006; ◊: .006. For (A), $P_{encounter} = .0006$. For (B), $P_{\mathrm{LL}} = .4$, $P_{\mathrm{HH}} = .8$.

The role of time budgets for environments with within-day variance is similar to that described for the other two environments we simulated: pilferage induces increased caching, which induces increased eating, which in turn decreases rest time (Figure 10A,B). Under some conditions, caching rates when the birds are interrupted appear to be constrained by a lack of resting time (e.g., Figure 10A,C). Birds will generally rest through the interruption (Figure 10B,D), with retrieval used only by very low-weight birds (data not shown).

The effect of predation risk on energy regulation under cache pilferage is similar to that seen with between-day variation. Generally, increased predation risk is predicted to cause a reduction in cache intensity, but not under all conditions (Figure 9B). The exception to this rule is caused by the birds eating more encountered food in "good" patches under the joint conditions of high pilferage rates and low predation risk (Figure 10E), instead of resting more under high pilferage rates and high predation risk (Figure 10C). Levels of predation risk have little effect on time budgets in "bad" patches; here birds should generally rest unless they are near starvation, in which case they will retrieve food (Figure 10D,F).

Finally, mean dawn mass levels are relatively unaffected by changes in the level of predation risk if the birds cache appreciable amounts of food then; otherwise body mass decreases with an increased predation risk (Figure 8C).

DISCUSSION

Earlier models of caching behavior predicted that cache investment would decrease monotonically as pilferage in-

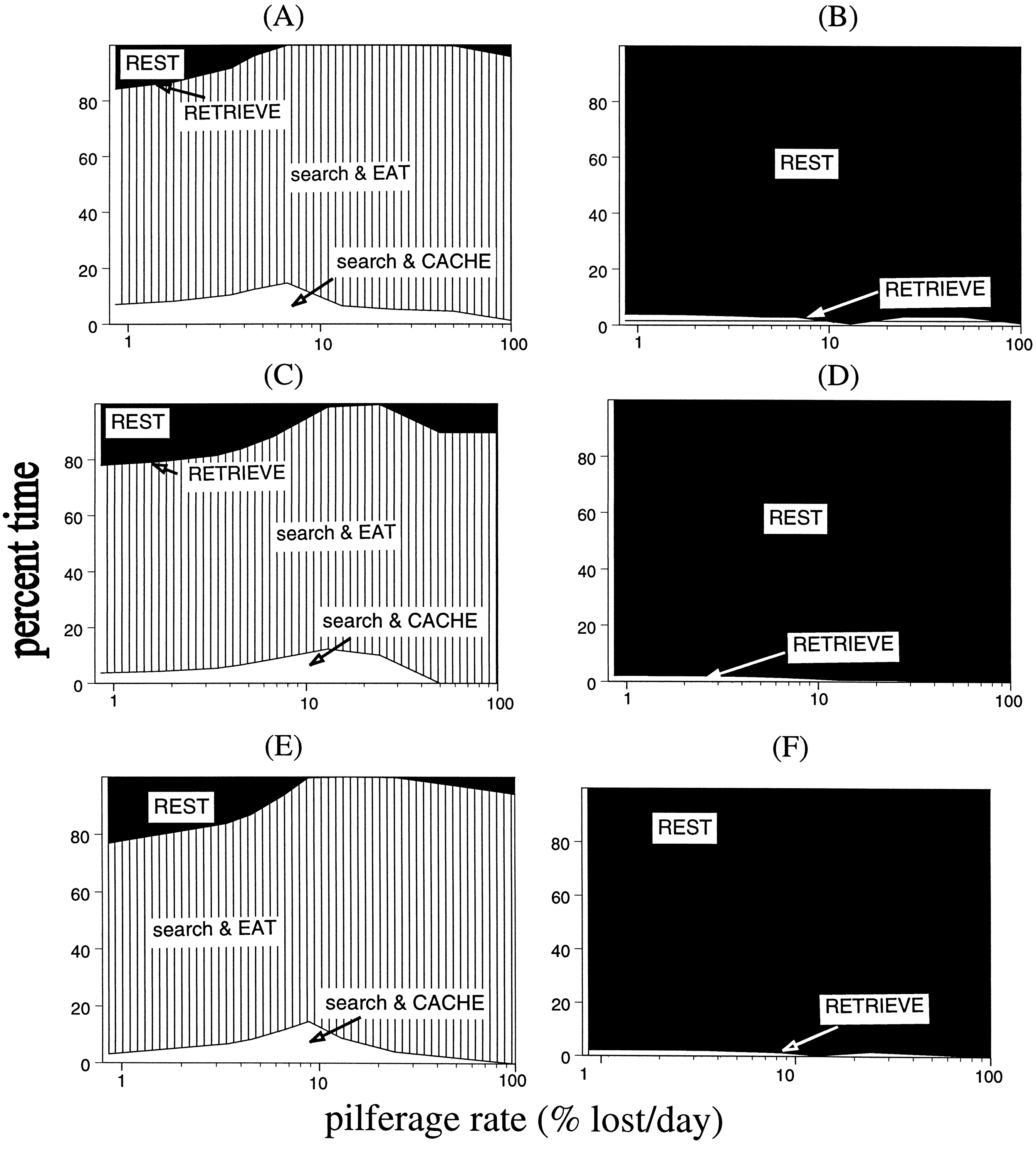

Figure 10
Predicted daily time budget as a function of pilferage rate for within-day variance in food encounter rates (see text). (A)–(D) illustrate the effect on time budgets of different levels of within-day variance. (C)–(F) illustrate the effect of predation risk on time budgets. Transition probabilities were $P_{LL} = .2$, $P_{HH} = .9$ in Figure (A) and (B); transition probabilities were $P_{LL} = .4$, $P_{HH} = .8$ in Figure (C)–(F). $P_{encounter}$ (see text) was .0006 for (A)–(D) and .00006 for (E) and (F). (A), (C) and (E) represent time budgets when the bird is in "good" patches; (B), (D) and (F) represent time budgets in "bad" patches. See text for description of interruptions and for definitions of variables.

creased. The results from our model do not support this prediction, irrespective of the environment type and food encounter rate we simulated. Instead, our results suggest that cache investment will peak at intermediate pilferage rates, even though cache size does decline monotonically with increased pilferage rate (Table 2). This statement holds whether cache investment is measured as the percent of food items cached per day or as the absolute rate of caching. Lucas and Zielinski (1998) suggested that the falsification of the prevailing prediction implied that we should reconsider the fundamental assumptions built into our dynamic models of caching behavior. However, the theoretical results described here suggest a less extreme conclusion: the previous models may not have incorporated sufficient detail to provide a robust understanding of the effect of pilferage rates on energy regulation patterns.

Our analyses suggest that we have been too simplistic in developing the logic of energy regulation. In particular, the joint regulation of the cache and internal energy stores includes tradeoffs between a number of variables. Fat storage should decrease starvation risk but increase metabolic rates and increase predation risk; this tradeoff is the focus of a large literature (Bednekoff and Krebs, 1995; Ekman and Hake, 1990; Houston et al., 1997; Lilliendahl et al., 1996; Lima, 1986; Pravosudov and Grubb 1997a; Witter and Cuthill, 1993). Cache storage involves similar starvation/predation risk tradeoffs (Källander and Smith, 1990; Lucas and Walter, 1991; McNamara et al., 1990; Pravosudov and Grubb, 1997a). The similarity in tradeoffs associated with these two forms of storage presumably led to the prediction that cache pilferage should cause a reduction in the reliance on the cache while concomitantly increasing reliance on fat reserves (Ekman and Lilliendahl, 1993; Lucas and Walter, 1991; McNamara et al., 1990; Sherry, 1985). However, cache storage incurs metabolic expenditures that in turn affect tradeoffs associated with the time budget, particularly with respect resting time (Table 2). Cache pilferage can induce increased caching rates that offset the loss to pilferage. This increase in time invested in caching comes at the cost of a reduction in time spent resting, and this shift in time budget is exacerbated by the increased energy expended while caching, which induces an increase in feeding rates. King and Murphy (1985) suggested that time budget manipulation can play a key role in energy regulation. Our results underscore the validity of this conclusion: time-budget tradeoffs are an important element in the adaptive response to cache pilferage but have been under-appreciated to date.

Increased metabolic costs associated with pilferage-induced caching are exacerbated by the effects of pilferage on fat regulation: fat reserves should increase to offset the increase in starvation risk caused by a pilferage-induced reduction in cache size (see Lucas and Walter, 1991). The increase in fat reserves will generate an increase in metabolic expenditure beyond the expense incurred from caching. At generally low pilferage rates, a marginal loss due to pilferage can profitably be offset by an increase in caching intensity at the expense of a reduction in resting time. However, beyond some threshold pilferage rate, the marginal value of rest becomes greater than the marginal value of caching behavior. The result is an increase in rest and a reduction in caching intensity with a further increase in pilferage rate. Similar results have been observed in rats and pigeons when the cost of obtaining food is increased (Schrader and Green, 1990).

Characteristics of the environment other than pilferage will also influence energetic tradeoffs. For example, if the bird faces between-day variation in food abundance, on ''bad'' days it can choose to rely primarily on retrieving cached food, or it can rely primarily on the search for uncached food. Obviously, cached food is more valuable at low pilferage rates and low food-encounter rates. Under some circumstances, this tradeoff may complicate the relationship between caching intensity and pilferage rates on ''good'' days (e.g., Figure 5B).

Similarly, the level of predation risk incurred while foraging or resting can complicate tradeoffs associated with time budgets and energy regulation patterns. For example, the presence of a unimodal relationship between cache intensity and pilferage rate (Table 2) assumes that there is a predator-safe refuge for resting birds. Instead if there is no refuge, then the bird will never rest, and energy regulation is the result of a simple tradeoff between caching and eating: as pilferage rate increases, birds are predicted to shift from a preference for caching to a preference for eating. Another example is the effect of varying levels of predation risk on the cache-intensity/pilferage-rate function. If predation risk while foraging is high, then birds are predicted to reduce caching and increase resting at high pilferage rates. In effect, the increased survival from predation derived from resting is greater than the increased survival derived from foraging at high pilferage rates. However, if predation risk while foraging is low, then birds are predicted to reduce caching and increase foraging at high pilferage rates. Here, foraging to eat is more valuable than rest at high pilferage rates. These effects of predation risk on the time budget will in turn complicate the relationship between predation risk and energy regulation patterns (e.g., Figure 5C and Figure 9B).

Our results can be used to address several aspects of a broader issue related to the tradeoff between cache and fat storage. Experimental evidence indicates that the physiological mechanisms of mass regulation and hoarding seem to share at least some neurophysiological components (e.g., Herberg and Blundell, 1970; VanderWall, 1990). This physiological linkage between forms of energy storage provides a mechanism for the general perception that cache regulation is an alternative to fat regulation (McNamara et al., 1990; Sherry, 1985). Indeed, the result of this joint regulation of cached food and fat reserves can be logically simple. For example, in rats and tufted titmice, caching rates decrease with an increase in body mass (Fantino and Cabanac, 1980; Lucas et al., 1993, but see Pravosudov and Grubb, 1997b, for the opposite trend in tufted titmice). However, the sign of the correlation between mass and caching intensity changes with overall levels of food availability in Carolina chickadees (Lucas, 1994). The correlation is negative when food is relatively abundant, because future energy reserves are devalued for relatively heavy birds foraging in ''good'' environments. However, the correlation is positive when food is scarce, because future energy reserves shift to become more valuable for relatively heavy birds foraging in harsh environments and shift to become less valuable for relatively lightweight birds. Clearly, the tradeoffs between the different forms of energy are environment dependent. The results described here provide another example of this point: as pilferage rates increase, mass should increase monotonically, but caching intensity should first increase then decrease. One consequence of this is that the relationship between body mass and caching intensity (measured across environments that differ in pilferage rates) should change sign with a change in pilferage rate.

Similar complications arise with expected energy regulation patterns under increasing mean food abundance. We noted earlier that under relatively abundant food supplies, increases in mean availability of food (holding variance constant) were predicted to cause an overall reduction in both cache size and fat reserves (Lucas and Walter, 1991; McNamara et al., 1990): an increase in food encounter rates decreases starvation risk which in turn reduces the need to store energy in any form. This general pattern has been empirically demonstrated for several species of parids (e.g., Lucas, 1994; Lucas et al., 1993; Pravosudov and Grubb, 1997b). This prediction seems robust for time-invariant resource variance (i.e., no variability between days and constant diurnal levels of variance). Not surprisingly, both Lucas and Walter (1991) and McNamara et al. (1990) simulated this type of resource variability. In contrast, if birds experience between-day variation in resource abundance, increased food availability on ''good'' days should trigger higher caching intensities, whereas no substantial changes in body mass were predicted. In effect, high food encounter rates on ''good'' days provide excess cachable food for ''bad'' days. At the same time, in contrast to time-invariant resource variance scenario, it may be disadvantageous to reduce fat reserves in these conditions because there is some probability of encountering a ''bad'' day with low food availability. On the other hand, increased food availability on ''bad'' days should trigger lower caching intensities, because the value of caching on ''good'' days diminishes when starvation risk on ''bad'' days is low.

A result from our model is that regulated fat levels may, under some circumstances, be insensitive to mean food encounter rates (holding pilferage rates fixed). Indeed, cache intensity and cache size appear to be more plastic than fat regulation under a number of conditions we simulated (e.g., changes in pilferage rate, food encounter rate, or level of predation risk). Hurly (1992) found this trend in an experiment on marsh tits (*Parus palustris*): an increase in food encounter rate (and concomitant decrease in variability) generated lower caching rates but no change in body mass. In another empirical study, Pravosudov and Grubb (1997b) found that tufted titmice increased both fat reserves and cache size in response to decreased food availability, thus underscoring the complexity of energy regulation tradeoffs.

In conclusion, the tradeoffs associated with energy regulation in caching animals can be quite subtle. Our model underscores the fact that we have much to learn about the nature of the tradeoffs faced by foraging animals making multidimensional decisions. For example, while a large literature has addressed the problem of foraging decisions in response to variability in the food supply (Kacelnik and Bateson, 1996), we show that the temporal scale of this variation can be critical in some aspects of energy regulation (e.g., overall cache size), but may have little effect in others (e.g., qualitative relationship between cache intensity and pilferage rate). In addition, these tradeoffs may be particularly complicated in cases where animals jointly regulate several types of energy stores (here the cache and body mass) that have fundamentally different dynamic properties. Further, our results may apply broadly to other classes of allocation decisions (e.g., parental resource allocation, Clutton-Brock, 1991, or mate provisioning, Moore et al., 2000) that have fitness consequences associated with the regulation of internal versus external energy demands.

Finally, the role that time budgets play in the behavioral ecology of energy regulation appears to have been under-appreciated. A detailed analysis of time budgets provides critical insight into number of the predicted relationships generated by our model (e.g., the unimodal relationship between caching intensity and pilferage rates), yet few studies of energy regulation include such analyses (e.g., see van der Veen, 1999). Our results suggest that the effort needed to include time budgets in these experiments is warranted.

This work was supported by the National Science Foundation under a Postdoctoral Research Fellowship in Biosciences Related to the Environment awarded in 1997 to V.V.P. We thank Peter Waser, Todd Freeberg, Jim Kellam, Karen Munroe, and Adam Boyko for their critiques of the manuscript. We would also like to thank David Westneat for an excellent job as editor of the manucript.

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