Why do hoarding birds gain fat in winter in the wrong way? Suggestions from a dynamic model

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In winter, small birds should be fat to avoid starvation and lean and agile to escape predators. This means that they face a trade-off between the costs and benefits of carrying fat reserves. Every day they must gain enough fat to survive the coming night. Food-hoarding species can afford to carry less fat than nonhoarders because they can store energy outside the body. Furthermore, hoarders should avoid carrying excessive fat during the day because they can gain fat fast by retrieving food late in the afternoon. With no stored supplies, nonhoarders face more unpredictable access to food, and they should start gaining fat earlier in the day. The predicted pattern is then that nonhoarders gain fat early and that hoarders gain fat late in the day. Recent field data show the opposite pattern: hoarders gain relatively more fat reserves in the morning than nonhoarders do. Using a dynamic model that mimics the conditions in a boreal winter forest, I investigated under which conditions this pattern will arise. The only assumption of those investigated that produced this pattern was to relax the effect of mass-dependent predation risk. I did this by introducing a limit under which fat reserves did not affect predation risk. Hoarders then started the day by gaining fat in the morning. Later, when they had reached a safer (but still not risky) level, they switched to hoarding. The pattern I searched would only occur if either not all food was possible to store, or if retrieval gave less energy than foraging in good weather conditions. If I assumed that low levels of body fat also increased predation risk, hoarders would cache in the morning when they carried least fat. I discuss empirical evidence for how body fat affects predation risk. In summary, the factors that produced the pattern I searched were a change in the predation-mortality function combined with restrictions on hoarding. *Key words:* dynamic modeling, fat reserves, food hoarding, *Paridae,* predation risk, stochastic dynamic programming. *[Behav Ecol 11:27–39 (2000)]*

Fat is the main body energy reserve for small birds, and they respond to winter conditions by increasing fat deposits (e.g., Haftorn, 1989; Lehikoinen, 1987; Rogers and Rogers, 1990; Smith and Metcalfe, 1997; Waite, 1992). Excessive body fat, however, may increase predation risk (e.g., King, 1972; Lima, 1986; Witter and Cuthill, 1993). First, heavier birds may be more at risk of being attacked by predator that depends on impaired takeoff ability (Hedenström, 1992; Lima, 1986; McNamara and Houston, 1990; Metcalfe and Ure, 1995; Kullberg et al., 1996; Witter et al., 1994). Also, fatter birds may have to spend more time foraging than leaner ones if metabolism is mass dependent (Houston and McNamara, 1993; Lima, 1986; McNamara et al., 1994; Witter and Cuthill, 1993), which will increase the time they may be exposed to predators. Hence, small birds in winter face a trade-off because they should minimize fat reserves with respect to predation risks and maximize them to avoid starvation (Clark and Ekman, 1995; Lima, 1986; McNamara and Houston, 1990).

That birds readily adjust fat levels in response to changes in predation risk has been interpreted as support for the importance of mass-dependent costs. However, after exposure to a predator, some species will decrease body fat reserves (Gosler et al., 1995, Lilliendahl, 1997b), whereas others will increase body fat (Lilliendahl, 1998, Pravosudov and Grubb, 1998) or fueling speed (Fransson and Weber, 1997), showing that the effect of fat reserves on predation risk may be complex.

Small birds typically gain 7–10 % extra body mass before a winter night (Haftorn, 1989; Lehikoinen, 1987). Empirical studies have measured the effect of body mass on takeoff ability and maneuverability, but this effect is still difficult to evaluate. In zebra finches *Taeniopygia guttata,* increases of only 7–8% body mass impaired spontaneous takeoff (Metcalfe and Ure, 1995). Because of small sample sizes, Metcalfe and Ure could not fully analyze predator induced takeoff. In two recent studies, Kullberg (1998) and Kullberg et al. (1998) examined predator-induced escape ability in willow tits, *Parus montanus,* and great tits, *P. major.* They found no effects of the 7–8% extra body mass that the birds gained on a daily basis. Witter et al. (1994) equipped starlings with artificial weights and startled the birds with an auditory stimulus. They found reduced takeoff ability for heavier birds in some experiments but no effect in others.

Food-hoarding species can store energy in the form of cached supplies, and these can be an alternative to body fat (Brodin and Clark, 1997; Hurly, 1992; Grubb and Pravosudov, 1994; Lucas, 1994; McNamara et al., 1990). If daily fat reserves of 7–8% do increase predation risk, theory predicts that hoarders should delay the buildup of fat deposits until late in the afternoon (McNamara et al., 1990). Nonhoarders, on the other hand, must build up supplies earlier in the day because they face more unpredictable access to food (McNamara et al., 1990).

Hoarding behavior under natural conditions in winter has been examined in the willow tit (Brodin, 1994; Haftorn, 1956). After a massive effort in the autumn (discussed by Brodin and Clark, 1997; Grubb and Pravosudov, 1994; Haftorn, 1956), when tens of thousands of seeds and nuts are stored, hoarding intensity is low in winter. Most days only a few items are stored, and a considerable part of the diet consists of food that rarely is stored (Brodin, 1994; Haftorn, 1956). The memory of caching locations seem to last only a week or so (Brodin
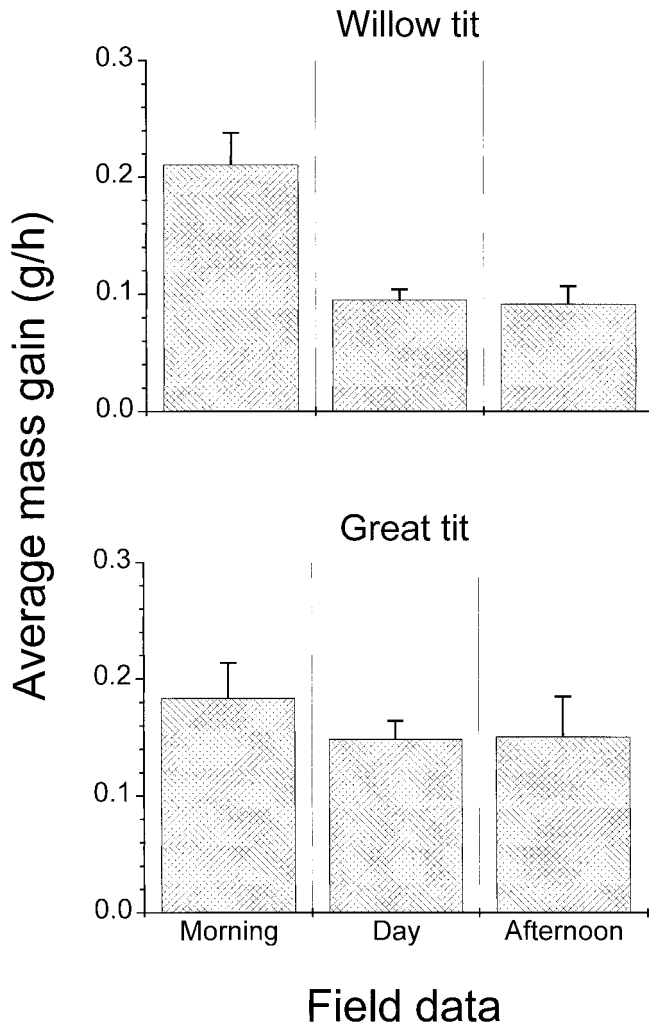
Figure 1
Average mass gain rate (g/h) in the willow tit ($n = 11$) and the great tit ($n = 9$) measured by Lilliendahl (1997a) in the field. Error bars are standard errors.

and Kunz, 1997), and only caches that are retained in memory can be comparable in availability to body fat. I refer to these caches that can be retrieved upon decision as short-term caches. Long-term caches are also important as an addition to the winter food supply (Brodin and Clark, 1997), but they require more search time and are less predictable in availability.

Recently Lilliendahl (1997a) measured how four species of small birds gain daily fat reserves in winter in south-central Sweden. Three of these were species that normally hoard food, the willow tit, the marsh tit, *P. palustris,* and the nuthatch, *Sitta europaea.* The fourth species was the nonhoarding great tit, *P. major.* Contrary to expectations, Lilliendahl found a significant peak in body mass gain rate in the morning in the three hoarding species that was not present in the great tit (Figure 1).

In the present study I used dynamic modeling to investigate under what parameter values the pattern of daily body mass gain observed by Lilliendahl (1997a) should arise. I concentrate here on body fat deposits and do not present results concerning stored supplies.

METHODS
Specifications of variables are listed in Appendix A and justification for values of parameters are given in Appendix B. The

model compares a hoarding to a nonhoarding strategy and is based on the following components. There are two time variables, $d,$ day in winter and, $t,$ time of day. D is then the length of winter, 100 days, and T the number of periods in 1 day, 3. I use $d = (0,1...D)$ to denote current day and $t = (1, 2,$ and $3)$ for current period, and I call these three periods "morning," "midday," and "afternoon." Even if there only are three periods, the precision in the model is sufficient for two reasons. First, each period is subdivided into proportions (without any time dimension) that can be allocated to the various activities. Second, stochastic changes in weather can only occur between the periods. For each period I save these proportions in a vector of decisions called the "behavior matrix."

All foraging activities and predation occur during day periods; nighttime metabolic costs reduce the bird's fat reserves. The model covers one winter, and it is assumed that maximizing fitness is equal to maximizing survival over this period.

During a period a bird allocates its time among four activities: (A) forage and eat all food found; (B) forage and store all food found (except if some food is unstorable, see below); (C) retrieve stored seeds; and (D) perch in a predator safe environment. All these activities are open to a hoarder, but A and D are the only options open to a nonhoarder.

Each activity (i) has a metabolic cost, $c_i,$ and a predation risk, $\mu_i.$ Both these increase linearly with fat reserves under baseline assumptions. Such maintenance costs are necessary to model regulation of fat reserves (Houston et al., 1997). I also introduce a limit, below which predation risk, $\mu,$ is not mass dependent. This limit can be set from 0 to 100% of the maximum fat reserve. I also examine the effects of quadratic increases in the effect of body mass on predation risk and metabolic cost. There are two state variables, body fat, $X(t),$ and stored seeds, $Y(t)$ (hoarders only); both are measured in kiloJoules. Hoarders remember the locations of stored seeds for a limited time and forget a constant fraction, $\gamma_3,$ each day. Furthermore, a hoarder can remember only a limited number of stored seeds.

I use the term "foraging behavior" rather than the conventional "foraging strategy" to describe how the current period's time allocation to activities A–D is specified in terms of the current time and state variables, t, X, Y (hoarders only), plus an stochastic parameter, $W,$ for weather conditions. I reserve the term "strategy" for being a hoarder or a nonhoarder.

Weather conditions, $W(t),$ may be either "good" or "bad" in a given period but change independently and unpredictably between periods. During one time period the foraging outcome is a rate of energy gain, which is reduced or even negative during periods with bad weather conditions. Bad conditions also can occur at night, but are unrelated to the weather during the day. Changing foraging behavior (e.g., by resting if weather gets bad) can counteract bad conditions during the day. There are no behavioral options during the night, and the only way to survive an unusually cold night is to carry large enough fat deposits before the night begins. In some runs of the model I include extra daytime stochasticity to investigate the effect of a varying energy gain from foraging. This variation cannot be met by changing foraging behavior like a period with bad weather. Instead, this extra stochasticity means that under given (good or bad) weather conditions the forager can have more or less luck in an unpredictable way.

In the model I consider only the optimal foraging behavior which maximizes the bird's probability of surviving the winter. Birds using either strategy will optimize their behavior by choosing the best activities from their given options. Even if nonhoarders only have two options, A and D, their behavior is still optimal. The model is primarily designed to investigate

Hoarder
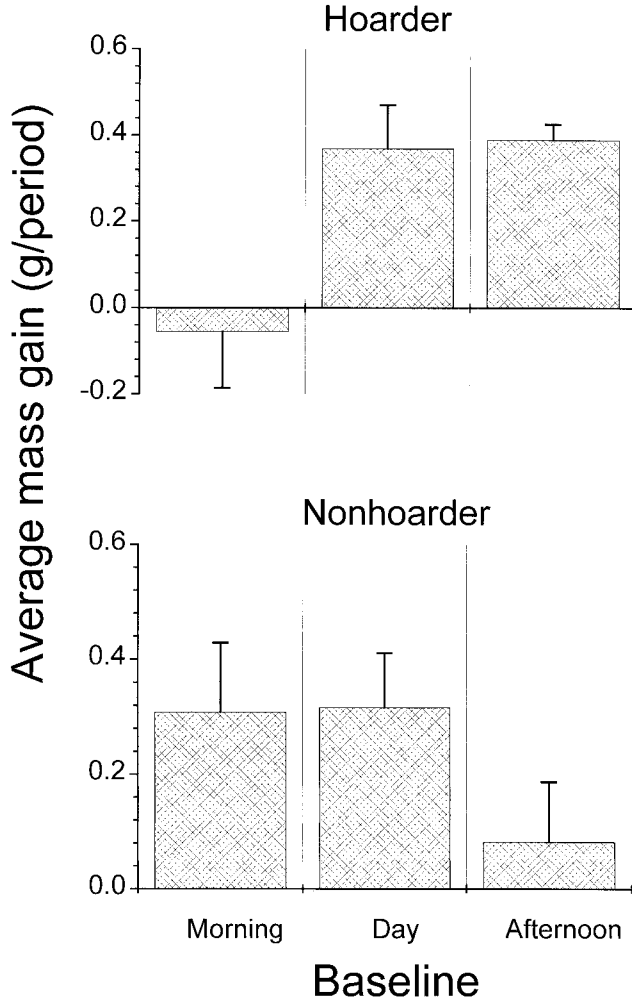
Nonhoarder

Figure 2
Average mass gain rate (g/period) for hoarders and nonhoarders under baseline assumptions (see Appendix B) in the model.

optimal behavior in hoarders, and two behavioral options may not be sufficient to predict realistic behaviors in nonhoarders. The threats to survival are starvation (which occurs if body reserves, X, fall below zero), and predation, which is stochastic.

I compute the optimal foraging behavior by dynamic programming (Houston et al., 1988; Mangel and Clark, 1988). First I iterate fitness backward from a known starting point; the survival probability is 1 if the bird is still alive the morning after the last day with $X(T+1) \geq 0$. For each time interval, the maximum survival probability will be the result of the optimal behavior at that time. For all possible combinations of variables (body fat, caches, and weather) the optimal behavior each period is saved in a behavior matrix. In the forward iterations I seed 1000 individuals from day 1 using this matrix. The starting condition, day 1, is 25% body fat and no cached food for hoarders.

I split each period in 10 discrete units that the forager can allocate to their given options (A–D) depending on whether it is a hoarder or not. For instance, the bird can spend 0, 1/10, 2/10 … 10/10 on activity A (forage and eat) in period 1, and so on. These proportions are the values actually saved in the strategy matrix. In a similar manner I divide the state variables (X and Y, or X only for nonhoarders) in discrete units from 0 to 20. Discrete values of variables, however, will make

calculations inaccurate because they will assume intermediate values. I therefore use linear interpolation for fitness values in the backward iteration and in order to determine optimal strategies in the forward iteration. For the interpolation of fitness values it should be noted that death by starvation does not occur at fat deposits $x = 0$ (as, for example, in Brodin and Clark, 1997) but at $x < 0$ (see Appendix A).

For the dynamic programming computations I use the following fitness functions for hoarders (h). The fitness functions for nonhoarders (n) are similar, except that they are denoted F_n instead of F_h, and they do not contain any variable for stored food, y. I show function 1 for both strategies and the rest for hoarders only. I annotate functions for hoarders $H1$, $H2$ … and the corresponding functions for nonhoarders $N1$, $N2$ … and so on.

$F_h(x, y, w, t, d) =$ maximum probability that the hoarder survives from the beginning of period t on day d to the morning of day $D + 1$, given that $X(t, d) = x$, $Y(t, d) = y$, and $W(t, d) = w$. (H1)

$F_n(x, w, t, d) =$ maximum probability that the nonhoarder survives from the beginning of period t on day d to the morning of day $D + 1$, given that $X(t, d) = x$, and $W(t, d) = w$. (N1)

$\tilde{F}_h(x, y, d) =$ maximum probability (evaluated before the night) that the hoarder survives from the evening of day d to the morning of day $D + 1$, given that $X(d) = x$, and $Y(d) = y$. (H2)

As mentioned above, X is body fat reserves, with its present value denoted x, and Y is stored supplies with its present value y. At the start of the night on day D, we then have:

$$\tilde{F}_h(x, y, D) = \begin{cases} 1 & \text{if } x \geq c_b(D) \\ p_{ng} & \text{if } c_g(D) \leq x \leq c_b(D) \\ 0 & \text{if } x < c_g(D), \end{cases} \quad \text{(H3)}$$

where $c_b(D)$ and $c_g(D)$ denote nighttime metabolic cost for good and bad nights (day D), and p_{ng} is the probability for a good night. This equation says that the bird will always survive the final night if its energy reserves, x, are $\geq c_b(D)$. It will survive with probability p_{ng} if x is $\geq c_g(D)$ but $< c_b(D)$. Finally, the bird will always die if fat reserves are $< c_g(D)$.

For $d < D$ and $t < T$ and $x \geq 0$, we have the following dynamic programming equations for good an bad weather conditions, respectively:

$F_h(x, y, w_g, d, t)$

$= \max_{\underline{a}} (1 - \mu_{\underline{a}}) [p_{wg} F_h(x'_{\underline{a}}, y'_{\underline{a}}, w_g, d, t + 1)$

$+ (1 - p_{wg}) F_h(x'_{\underline{a}}, y'_{\underline{a}}, w_b, d, t + 1)]$ (H4)

$F_h(x, y, w_b, d, t)$

$= \max_{\underline{a}} (1 - \mu_{\underline{a}}) [p_{wg} F_h(x''_{\underline{a}}, y''_{\underline{a}}, w_g, d, t + 1)$

$+ (1 - p_{wg}) F_h(x''_{\underline{a}}, y''_{\underline{a}}, w_b, d, t + 1)].$ (H5)

This is for coupling time-periods when $t < T$ during day d. Here $\underline{a} = (a_A, a_B, a_C, a_D)$, a_A is the proportion of the period spent in activity A, and $(a_A + a_B + a_C + a_D) = 1$. The variable w here assumes the value w_g (good weather) or w_b (bad weather). Also, $x'_{\underline{a}}$ is the level of body fat reserves at the end of period t if weather is good. This is under the assumption that

the level was x at the beginning of the period and that activities during the period are spent according to $\underline{a}$. For a bad weather period, fat reserves become $x''_{\underline{a}}$ at the end of the period. The same notation applies for $y'_{\underline{a}}$ and $y''_{\underline{a}}$, levels of hoarded energy. For the last period (T) of the day, the corresponding equations for good and bad weather are

$$F_h(x, y, w_g, d, T) = \max_{\underline{a}} (1 - \mu_{\underline{a}}) \tilde{F}_h(x'_{\underline{a}}, y'_{\underline{a}}, d) \qquad (H6)$$

$$F_h(x, y, w_b, d, T) = \max_{\underline{a}} (1 - \mu_{\underline{a}}) \tilde{F}_h(x''_{\underline{a}}, y''_{\underline{a}}, d), \qquad (H7)$$

which couples the last period of day d to the night the same day. For coupling night to the next day, we have

$$\begin{aligned}
\tilde{F}_h(x, y, d) = p_{ng}[&p_{wg}F_h(x - c_g, w_g, y, d + 1) \\
&+ (1 - p_{wg})F_h(x - c_g, w_b, y, d + 1)] \\
+ (1 - p_{ng})[&p_{wg}F_h(x - c_b, w_g, y, d + 1) \\
&+ (1 - p_{wg})F_h(x - c_b, w_b, y, d + 1)]
\end{aligned}$$

$$\text{(H8)}$$

Also

$$F_h(x < 0, y, w, d, t) = 0. \qquad (H9)$$

Finally, the equations when energy gain varies unpredictably are in accordance with equations $H4$–$H9$, but with two possible outcomes for each weather type. As examples I show the equations that correspond to $H4$ and $H5$:

$$F_h(x, y, w_g, d, t)$$
$$\begin{aligned}
= \max_{\underline{a}} (1 - \mu_{\underline{a}}) (&p_{wg}(\lambda F_h(x'_{\underline{a},\text{high}}, y'_{\underline{a},\text{high}}, w_g, d, t + 1) \\
&+ (1 - \lambda)F_h(x'_{\underline{a},\text{low}}, y'_{\underline{a},\text{low}}, w_g, d, t + 1)) + (1 - p_{wg}) \\
\times (&\lambda F_h(x'_{\underline{a},\text{high}}, y'_{\underline{a},\text{high}}, w_b, d, t + 1) \\
&+ (1 - \lambda)F_h(x'_{\underline{a},\text{low}}, y'_{\underline{a},\text{low}}, w_b, d, t + 1)) \qquad (H10)
\end{aligned}$$

$$F_h(x, y, w_b, d, t)$$
$$\begin{aligned}
= \max_{\underline{a}} (1 - \mu_{\underline{a}}) (&p_{wg}(\lambda F_h(x''_{\underline{a},\text{high}}, y''_{\underline{a},\text{high}}, w_g, d, t + 1) \\
&+ (1 - \lambda)F_h(x''_{\underline{a},\text{low}}, y''_{\underline{a},\text{low}}, w_g, d, t + 1)) + (1 - p_{wg}) \\
\times (&\lambda F_h(x''_{\underline{a},\text{high}}, y''_{\underline{a},\text{high}}, w_b, d, t + 1) \\
&+ (1 - \lambda)F_h(x''_{\underline{a},\text{low}}, y''_{\underline{a},\text{low}}, w_b, d, t + 1)). \qquad (H11)
\end{aligned}$$

Here λ is the probability of good foraging luck (given good or bad weather). $x'_{\underline{a},high}$ is the new value of body fat reserves after successful (= good luck) foraging under good weather conditions, $x'_{\underline{a},low}$ is the value after unsuccessful foraging under good weather conditions, $x''_{\underline{a},high}$ is the value after successful foraging under bad weather conditions, and $x''_{\underline{a},low}$ is the value after bad luck under bad weather conditions. The notation for y is similar. Weather conditions have a larger effect than foraging luck on the amount of energy gained. This means that for a given time of foraging, $x'_{\underline{a},low}$ will be the highest possible value of body fat in the next time period, $x''_{\underline{a},low}$ the second highest, $x''_{\underline{a},high}$ the third, and $x''_{\underline{a},low}$ will be the lowest. Under baseline assumptions there is no net gain from foraging, and latter two will be lower than x.

In the forward iterations I seed 1000 individuals into the behavior matrix. Unless otherwise stated the dispersal measure is standard deviation.
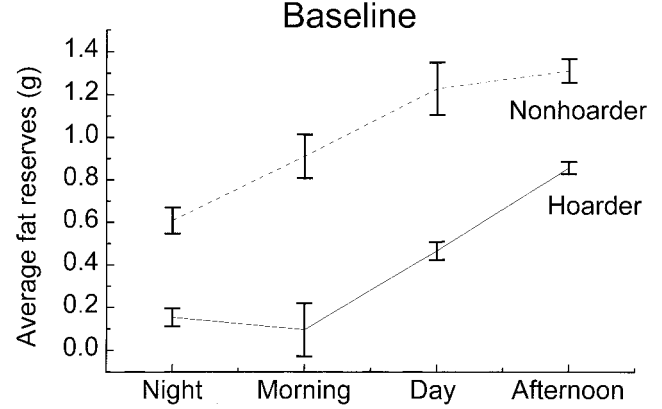

Figure 3
Average body fat reserves (g) for hoarders (solid line) and nonhoarders (dotted line) under baseline assumptions.

RESULTS

### Mass-dependent predation and poor retrieval

Under baseline parameters (Appendix B), the hoarder loses fat during the morning and gains mass evenly during the next two periods (Figure 2). The nonhoarder increases more in the two first periods than in the afternoon. During the whole day, the hoarder consistently carries lower reserves than the nonhoarder (Figure 3). The hoarder spends the morning storing and metabolizes reserves during this activity (Figure 4, top).

If I introduce a limit (ω) of 0.8 g of fat reserves, under which body mass does not affect predation risk, I get the pattern of mass gain in hoarders that Lilliendahl (1997a) observed in the field (Figure 5). Hoarders gain most fat in the morning and less in the two following periods. Now the hoarder spends most of the morning eating and stores most supplies during the midday period (Figure 4, middle). The rationale for the choice of limit is that 0.8 g is what birds such as willow tits and marsh tits normally carry before a winter night in the field (e.g., Haftorn, 1989; Kullberg, 1998; Lilliendahl, 1997a). I call the 0.8-g limit, together with other parameters at baseline level, "fieldlike assumptions." Although the hoarder's pattern corresponds closely to Lilliendahl's observations, the nonhoarder gains much during the two first periods but less in the afternoon.

The baseline assumption that only 50% of the encountered food can be stored reduces the profitability of hoarding compared to foraging and eating fresh food. Other restrictions on hoarding in combination with the 0.8-g limit might also produce the mass gain pattern I searched. One such plausible restriction would be to limit the energy gain from retrieval. In nature this would be the case if caches were few and spread out over a large area. If all food that is found can be stored ($\gamma_2 = 1.0$ instead of baseline 0.5), a "low retrieval" case ($\gamma_1 = 0.8$ instead of baseline 2.0) will give a pattern when hoarders also gain mass at the highest rate in the morning (Figure 6, top). With no restrictions on hoarding ($\gamma_1 = 2.0$ and $\gamma_2 = 1.0$), the hoarder gains fat evenly over the day, the midday rate being slightly higher than the rates in the two other periods (not shown).

If both of the restrictions on hoarding are applied simultaneously ($\gamma_1 = 0.8$ and $\gamma_2 = 0.5$) and a predation risk for retrieval is introduced ($\mu_C = 0.5\mu_A$), the pattern looks almost identical to Lilliendahl's field data (Figure 6, bottom). I call these conditions "worst case hoarding" because they will be least favorable for hoarding. In addition to predation risk also for retrieval hoarding is now restricted both by the facts that
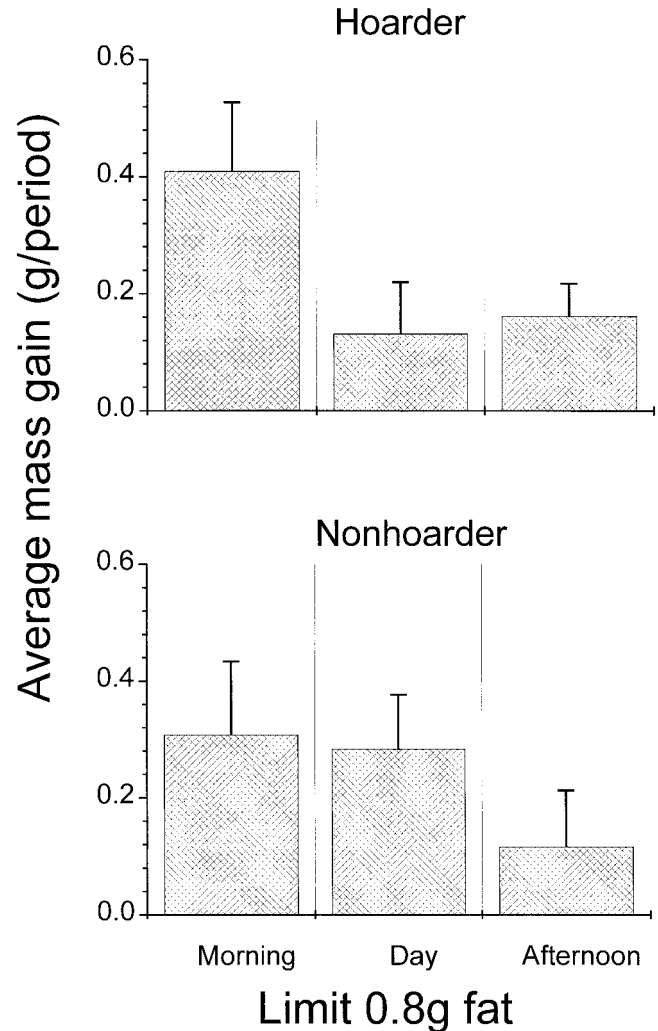
Worst case hoarding

Legend:
- Eat
- Store
- Retrieve
- Rest

Baseline

Fieldlike assumptions
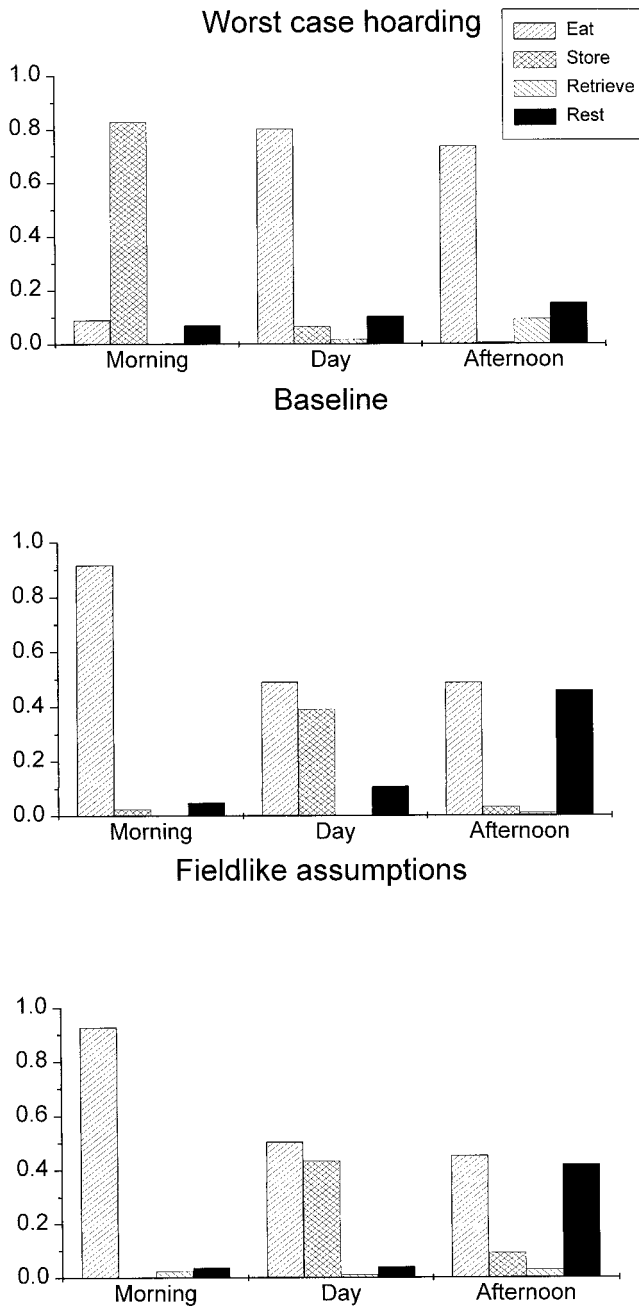
Figure 4
Proportion of time spent by the hoarder on the various behaviors under baseline and fieldlike assumptions (see Figure 5).
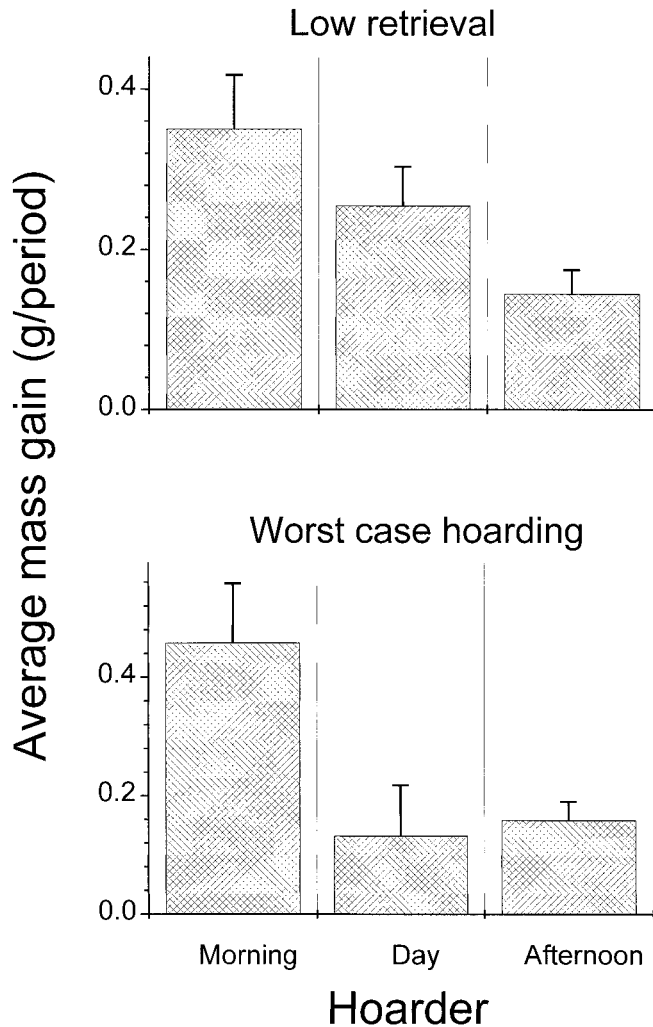
Hoarder

Nonhoarder

Limit 0.8g fat

Figure 5
Average mass gain rate (g/period) when a limit for mass-dependent predation of 0.8 g is introduced. The pattern resembles Lilliendahl's (1997a) observations from the field and is called the "fieldlike assumption.

Other parameters

I now investigate if changes in other parameters can produce the fieldlike pattern without the limit for mass-dependent predation risk. I remove the ω limit and return to the baseline assumption that predation risk increases linearly with body mass. With higher mass-dependent cost of activities ($\gamma_4 = 6.0$ instead of 2.5), the nonhoarder gains fat more evenly over the day, but this hardly affects the pattern of the hoarder at all (data not shown).

Changes in predation risk have clear effects. If predation risk increases from $\mu = 0.001$ to 0.005 and the mass-dependence constant, γ_5, increases from 10 to 25, the nonhoarder keeps the fat deposits before night almost as low as the hoarders, but the pattern of mass gain differs between the strategies (Figure 7).

The variability of the environment should affect the decision of how much fat a forager should carry. If unsuitable daytime weather becomes more frequent (the probability for good weather during a period being 0.8 instead of 0.95), both strategies will gain mass at an even rate during all three daytime periods. Both strategies now carry larger reserves, with the nonhoarder still carrying more fat than the hoarder (Fig-

only 50% of the encountered food can be stored and that retrieval only gives 80% of the energy that searching for new food would give. Still, stored supplies must be valuable as insurance because 43% of the midday period is allocated to storing (Figure 4, bottom), and mortality is only 11% for hoarders compared to 23% for nonhoarders (data not shown).

Under most conditions that I investigated the stored supplies will vary between 70% and 95% of maximum; that is, 35 to 47.4 kJ (not shown). Birds at low fat levels retrieve caches, and most retrieval occurs during period 3 under bad weather conditions (Table 1). Under the poor retrieval conditions (see above) birds will retrieve only if weather is bad.

Low retrieval

Worst case hoarding

Hoarder

Figure 6
Upper plot: average mass gain rate for hoarders (g/period) when reduced retrieval ($\gamma_1 = 0.8$ instead of 2.0) affects the profitability of hoarding and it is possible to store all encountered food ($\gamma_2 = 1.0$ instead of 0.5); ω is at 0.8 g fat. Lower plot: average mass gain rate for hoarders when conditions are least favorable for hoarding ($\gamma_1 = 0.8$, $\gamma_2 = 0.5$, and μ_C, the predation risk for retrieving, is $0.5\mu_A$ instead of 0).

ure 8). More nighttime variance will produce a pattern similar to the baseline case, but with both strategies carrying more fat (data not shown). If both day- and nighttime variances increase, the result is a linear pattern similar to that shown in Figure 8 but with slightly larger fat reserves (data not shown).

The amplitude of the daytime variation was large under baseline assumptions because bad weather during a period meant that no new food was found. Relaxing this assumption so that $r_a(w_b) = 0.5[r_a(w_g)] = 35$ kJ/day (given that the whole day is spent foraging) gives a pattern in which hoarders maintain slightly lower fat reserves during morning and midday than in the baseline case. Nonhoarders maintain lower fat reserves during all three periods, and both strategies show lower variation in fat levels and fat gain (data not shown).

If both night- and daytime conditions are constant, the hoarder stays at almost zero fat during the morning (Figure 9). Also, the nonhoarder now delays some of its mass gain until later in the day, but the pattern is not as extreme as for the hoarder.

How robust is the fieldlike pattern?

A sensitivity analysis of the limit for mass-dependent predation with other parameters at baseline level shows that this pattern will occur only at fat deposits between $\omega = 0.8$ g and 1.0g (Figure 10). A lower limit means approaching baseline conditions, and it will make the hoarder keep fat deposits low in the early part of the day and then gain needed fat later (Figure 10). At higher limits there is less incentive to keep evening fat low, as it is possible to carry more fat without increasing predation risk (Figure 10).

The limit had to be combined with a limitation on how much food can be stored or retrieved in order to obtain the fieldlike pattern. One such assumption was a low reward from retrieval ($\gamma_1 = 0.8$). Varying the values of γ_1 (0.2–0.9) show that the pattern is stable as long as retrieval gives less energy than foraging for new food (data not shown). A similar analysis of the effect of changes in γ_2 for values between 0.2 to 0.9 show that the pattern with most mass gain in the morning will arise as long as the proportion of the encountered food that can be stored, γ_2, is <0.9.

The fieldlike pattern may be specific to certain climatic conditions (e.g., it may appear only when winter nights are cold). Lowering the energy loss during normal nights from 29 to 14 kJ shows that this is not the case (Figure 11). Both strategies now gain almost all needed fat in the morning, and nonhoarders now follow almost exactly the same gain curve as hoarders (Figure 12). Relaxing the assumption that bad weather gives no new food [$r_a(w_b) = 35$ kJ/day] gives a similar pattern as shown in Figure 11, with both strategies gaining most fat in the morning. Milder nights will also make the mass gain pattern robust for a wider range of limits. The pattern with most mass gain in the morning is then stable for the limits from $\omega = 20$ kJ and upward in Figure 10.

A more severe climate can be introduced by making nights colder (energy loss 31 instead of 29 kJ). This will give a similar pattern as Figure 5 but with both strategies carrying more fat (not shown). The hoarder will then forage more intensively in the afternoon to gain this extra fat (not shown). A harsher environment can also be modeled by decreasing the energy gain rate when foraging. An r_a of 60 instead of 70 kJ/day will produce a pattern where both strategies gain mass evenly over the day (data not shown).

The state variables x and y are divided into 20 discrete units, and each time period during the day is divided into 10 units. If the grid is too coarse, this may affect the model in an undesired way. I made sensitivity tests of the discretization of the state variables from 10 to 25 units to ensure that this was not the case. If I decrease the number of units of x to 10, the fat gain pattern changes so that the gain rate is equally high in the two first periods (data not shown). Gradually increasing the number of units of x shows that at 15 units the mass gain pattern resembles the one at 20 and then remains stable at further increases. The variable y is less sensitive than x: decreasing the number of units to 10 hardly affects the patterns at all (data not shown). Increasing the number of units of x or y up to 25 will not have any discernible effects on the results. Furthermore, the linear interpolation reduces the problem with discrete units. Ten discrete units within each time period should be more than sufficient because only five units will still give almost the same results. The main effect of more than 10 time units is to slow down the computer runs, with results remaining the same.

Nonlinear effects of body mass on predation or metabolic costs may produce a different pattern. Bednekoff (1996) showed that adding just one factor, scanning behavior of the prey, is sufficient to make an assumed linear effect on predation risk accelerating. A quadratic metabolic cost will only

Table 1

Proportion of time spent retrieving stored food under three different conditions: baseline, fieldlike, and low retrieval ($\gamma_1 = 0.8$)

Fat (g)	Baseline Good	Baseline Bad	Fieldlike Good	Fieldlike Bad	Low retrieval Good	Low retrieval Bad
Period 1						
0	0.0	0.1	0.0	1.0	0.0	1.0
0.06	0.0	0.0	0.0	1.0	0.0	1.0
0.12	0.0	0.0	0.0	0.2	0.0	0.2
0.19	0.0	0.0	0.0	0.2	0.0	0.0
0.26	0.0	0.0	0.0	0.0	0.0	0.0
Period 2						
0	0.0	0.4	0.0	1.0	0.0	1.0
0.06	0.0	0.4	0.0	1.0	0.0	1.0
0.12	0.0	0.3	0.0	1.0	0.0	1.0
0.19	0.0	0.1	0.0	0.9	0.0	0.8
0.26	0.0	0.0	0.0	0.6	0.0	0.6
0.32	0.0	0.0	0.0	0.3	0.0	0.3
0.38	0.0	0.0	0.0	0.0	0.0	0.0
Period 3						
0	0.7	0.9	0.0	0.0[a]	0.0	0.0[a]
0.06	0.5	0.9	0.0	0.0[a]	0.0	0.0[a]
0.12	0.3	0.7	0.0	0.0[a]	0.0	0.0[a]
0.19	0.1	0.6	0.0	1.0	0.0	1.0
0.26	0.0	0.5	0.0	1.0	0.0	1.0
0.32	0.0	0.4	0.0	0.9	0.0	0.9
0.38	0.0	0.2	0.1	0.6	0.0	0.6
0.45	0.0	0.1	0.0	0.3	0.0	0.3
0.51	0.0	0.0	0.0	0.0	0.0	0.0

See text for more details on conditions. Good and bad are weather conditions. Fat levels can vary in 20 steps from 0 up to 1.3 g, but for fat levels not shown retrieval is 0. Periods 1 (morning) to 3 (afternoon) are shown from top to bottom.

[a] There is no optimal strategy since individuals with these low fat reserves will die overnight.

have small effects on the mass gain pattern (Figure 13) provided that costs are similar as in the baseline case ($\gamma_4 = 10$, Figure 14, top). A quadratic effect of fat reserves on predation risk (Appendix A) of the same magnitude as the baseline cost ($\gamma_5 = 5$) gives a pattern similar to the fieldlike pattern (data not shown). Observe, however, that there still has to be a limit ω at 0.8 g making the effect of fat on predation risk similar as under the assumptions that produced the fieldlike pattern (Figure 14, bottom). With no limit for mass-dependent predation, a quadratic predation cost for all fat reserves will give

a pattern of mass gain similar to that under baseline assumptions (Figure 2).

With the introduction of λ (see Equations H10 and H11), there is additional stochasticity because foraging luck may vary also if the weather conditions are known. If bad foraging luck means a reduction of 14 kJ, 20% of $r_a(w_g)$, and λ at 0.9, the pattern is almost identical to that in Figure 5 (data not shown).

DISCUSSION

The effect of fat deposits on predation risk

Of the parameters I tested, the only one that would make hoarders gain fat at the highest rate in the morning was a limit for the effect of mass dependence on predation risk. This limit was important regardless of whether the risk increased in a linear or quadratic way with body mass. A prerequisite was that there also was some limitation on either building up or using hoarded food. This could be either that not all encountered food is storable or that the mean rate of energy gain from retrieval is lower than the one obtained when searching for new food. In conclusion, the factors that produced the pattern I searched were a change in the predation-mortality function combined with restrictions on hoarding.

The fieldlike pattern was robust against changes in the hoarding parameters (γ_1 and γ_2), the coarseness of the grid, and the climate parameters. The pattern would also remain the same under nonlinear effects of body mass on predation risk and metabolic costs provided that the effects were of a
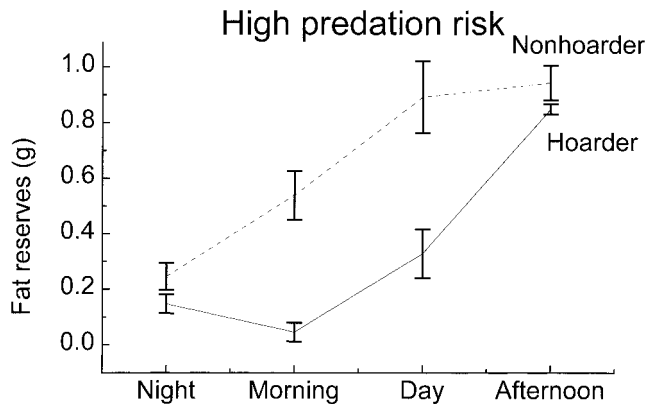
Figure 7
Average fat reserves (g) under increased predation risk ($\mu = 0.005$/day instead of 0.001/day and $\gamma_5 = 25$ instead of 10).
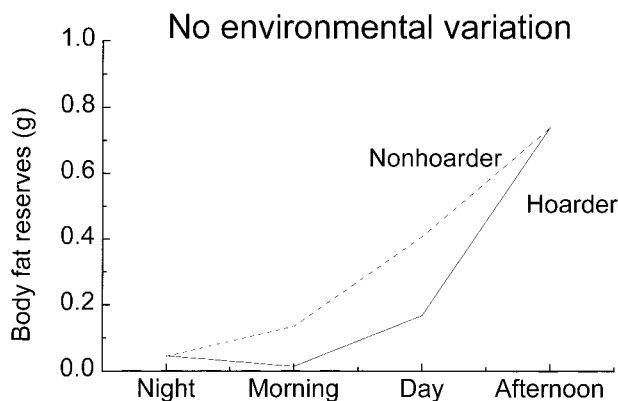
High daytime variance
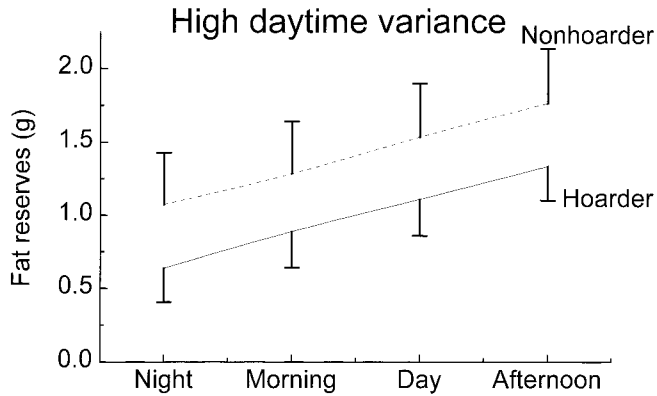
Figure 8
Average fat reserves (g) when daytime variance is increased compared to baseline conditions (the probability of bad weather is 0.2 instead of 0.05).

Figure 10
The effect of increasing the limit, ω, for mass-dependent predation risk stepwise from 0 to 1.3 g fat. Bottom curve, ω = 0 kJ (0 g), second curve 10 kJ (0.26 g), third curve 20 kJ (0.51 g), fourth curve 30 kJ (0.77 g), fifth curve 40 kJ (1.0 g), and top curve 50 kJ (1.3 g). The pattern with most increase in the morning and less later in the day only occur in curves 3 and 4.

similar magnitude as under the baseline assumptions. The pattern was sensitive for changes in ω (the predation free limit) and occurred between 20 and 30 kJ (0.51–0.77 g) in a test with 10-kJ steps. However, with my baseline values of the parameters, I force the birds up close to this limit. If I relax the energetic requirements (milder nights or positive gain of energy also when foraging under bad weather conditions), the range of limits that will give a fieldlike pattern gets wider.
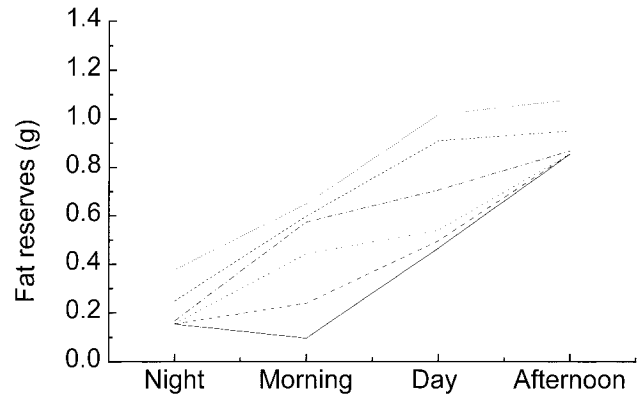
My assumptions about the effect of body mass on predation risk are in accordance with the experimental results of Kullberg (1998) and Kullberg et al. (1998). These suggest that there is no effect in willow tits or in great tits on the ability to takeoff for fat loads of 7–8%. Kullberg et al. (1996) found a clear effect on takeoff ability in blackcaps, *Sylvia atricapilla,* but this was for larger fat reserves. The blackcaps gained up to 60% fat during the experiment, and both takeoff angle and velocity were reduced.

The study on zebra finches by Metcalfe and Ure (1995) suggests that small fat loads should also impair escape ability. There could be a species difference depending, for example, on if zebra finches carried more fat than arboreal tits before the daily fat gain in the morning. The difference could also depend on methodology. Metcalfe and Ure mainly analyzed spontaneous takeoff, whereas Kullberg (1998) and Kullberg et al. (1998) measured predator-induced take off. At spontaneous takeoff, energetic economy rather than maximum acceleration should be optimized. Recently the effect of body mass on escape ability in zebra finches has been depreciated for alarmed birds (Veasy et al., 1998).
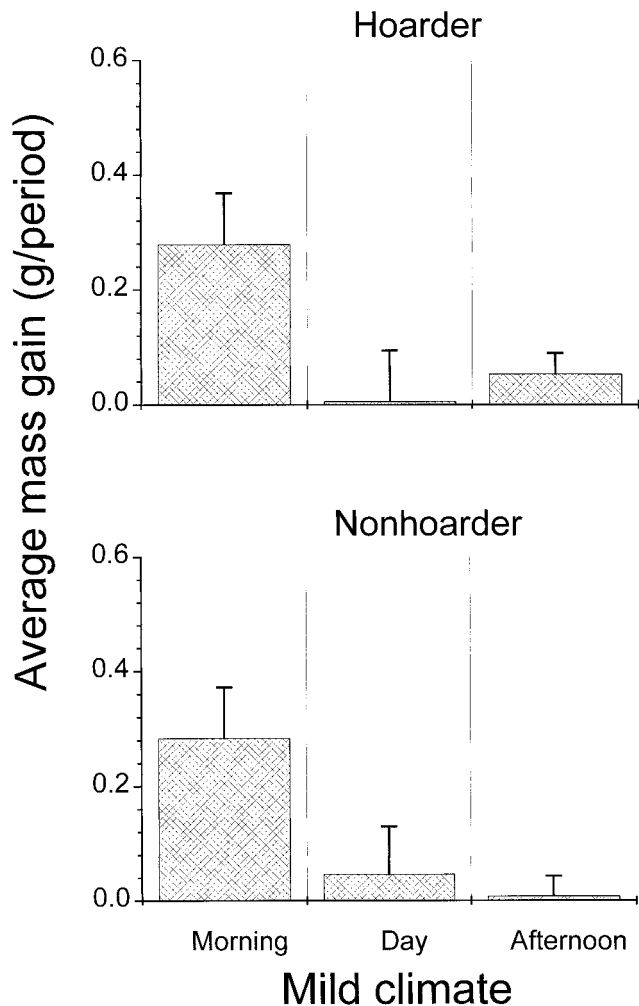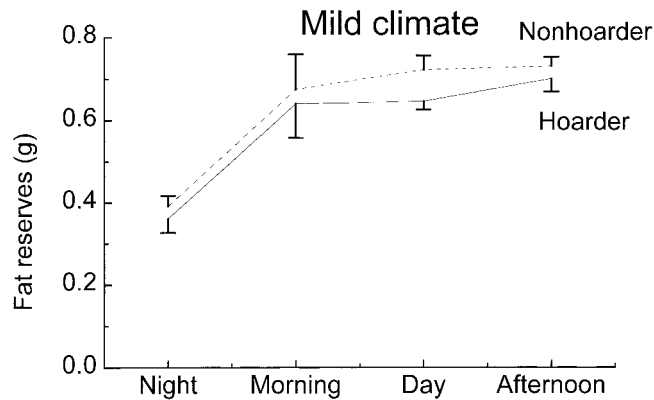
No environmental variation

Figure 9
Average fat reserves (g) under constant weather conditions.

Figure 11
Average mass gain rate (g/period) for hoarders and nonhoarders if nights are milder (energy loss 14 rather than 29 kJ for a normal night).
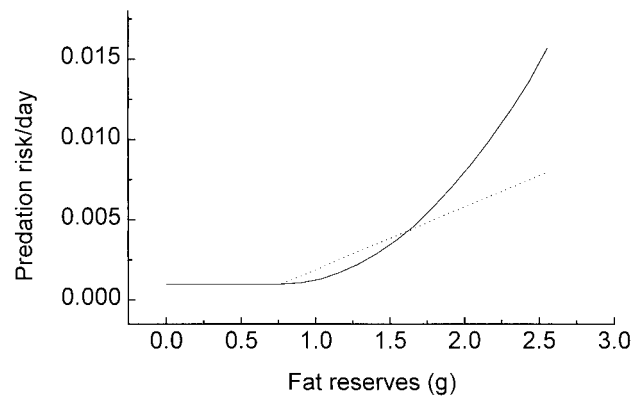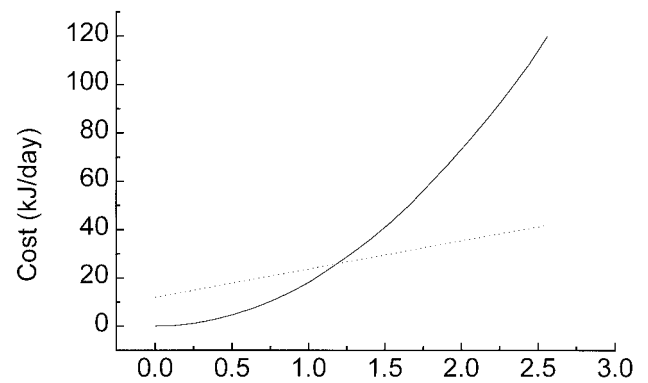
Figure 12
Average fat reserves (g) under the same conditions as in Figure 11.

Is it possible, then, that predation risk could remain unaffected by increases in body mass? First, measured takeoff speed may not be the same as the currency that really affects fitness, experienced predation risk. Factors such as rank, position in the foraging party, time available for scanning, knowl-
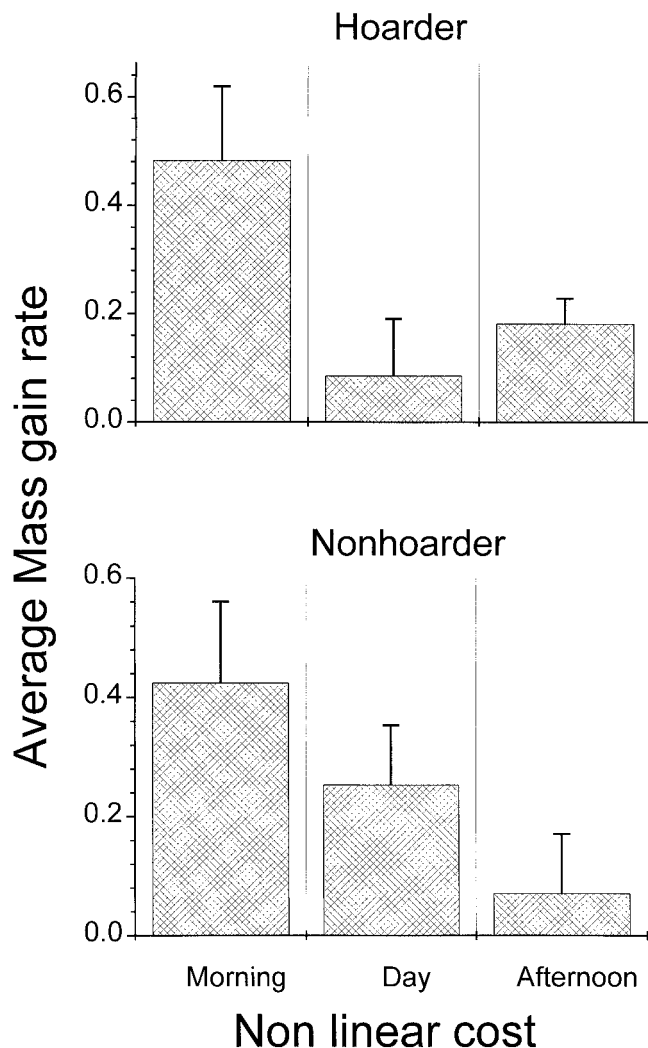
Figure 13
Average mass gain (g/period) when metabolic cost increases in a quadratic way with fat reserves.

Figure 14
Linear (dotted line) and quadratic (solid curve) effects of body mass on metabolic cost (upper plot) and predation risk (lower plot) given that $a_A = 1$. Equations and parameter values are in the appendices.

edge of the environment, and so on, could be more important for the probability of escaping an attacking predator and make small differences in flight speed less important.

Kullberg's (1998) and Kullberg's et al. (1998) experiments measured takeoff parameters such as speed, acceleration, and angle rather than experienced predation. According to physical laws, with other factors unchanged, flight speed must decrease when body mass fat increases. A possible explanation would be that fatter birds to some extent compensate for this by gaining more muscular tissue in the flight muscles (e.g., Lilliendahl, 1997a). Such a compensation has been reported during migration fattening in some species (Fry et al, 1972; Lindström and Piersma, 1993).

Another possibility is that the birds in the experiments did not always fly at full speed. An example could be if optimal acceleration during escape flight is lower than the maximum acceleration, perhaps in order to allow for better evasion maneuverability.

The pattern of mass gain explained

If we assume that there is a limit for mass-dependent predation, why would this make hoarders gain fat at the highest rate in the morning? By relying on the stored supplies, hoarders can afford to keep fat reserves low to stay under the level of increased predation risk. In the evening hoarders carried a mean of 0.93 g fat, which is the daily gain plus a small morning reserve. This can be compared with the 0.74–0.89 g that is metabolized overnight. If conditions are bad the following morning, hoarders can retrieve stored caches. Non-

hoarders do not have this option and must carry larger fat reserves in the morning.

Starting the day with almost no reserves, hoarders begin by gaining fat to hedge against poor foraging conditions later in the day. Before reaching the limit where fat reserves increase predation risk, the birds start hoarding during midday. Contrasting to this were the baseline assumptions when small levels of fat also increased predation risk. Then it was important to be as light as possible when storing and hoarding occurred early in the morning.

While my fieldlike assumptions give the pattern I searched for hoarders, nonhoarders gain most in the first two periods and little in the last period under most values of parameters. Great tits gained fat at an almost even rate in the field (Figure 1). Observe, however, that under most values of parameters in the model, nonhoarders will lose energy in bad weather because they cannot retrieve. Having only two foraging options (forage or rest) may not be realistic. It forces the non-hoarders to secure needed fat before the last period of the day in case weather should become bad. Also, a harsher environment (smaller r_A) evens out the gain. It is possible that the coniferous winter forest is a harsher environment for the great tit than for the other species. The three hoarding species are all year-round residents in their territories, but the great tit is more nomadic in winter.

Could factors not considered in the model explain the mass gain pattern?

The proportional fat level that is optimal should differ for species of different body size. The nonhoarder in Lilliendahl's study, the great tit, is a larger bird than the two hoarding parids, willow and marsh tits. The fourth species, however, is the hoarding nuthatch, of similar size and larger body mass than the great tit. The nuthatch showed the same mass gain pattern as the other hoarders (Lilliendahl, 1997a). It is thus unlikely that the different mass gain pattern showed by the great tit depends on size differences. In addition, all birds were studied during the same time of year in the same area, so it is unlikely that the difference in pattern would have been caused by differences in food supply or weather.

A reduction in overnight body temperature, or nocturnal hypothermia, means that starvation can be avoided if, for example, the fat supplies were exhausted during a cold night. Field data (Haftorn, 1972) suggest that hypothermia might be more developed in northern species such willow tits and Siberian tits *P. cinctus*. Species with a more developed ability to enter hypothermia can afford to keep lower fat reserves than other species. This could be a reason for interspecific differences in the daily pattern of fat gain. The difference in Lilliendahl's study, however, is between the great tit and the three hoarding species, not between the northernmost (willow tit) and the three more southern species.

Should hoarders always show this diurnal pattern?

Under my fieldlike assumptions, hoarding intensity peaked in midday, whereas it peaked in the morning under baseline assumptions. If the morning is allocated to hoarding, this means that no or little body mass will be gained. In an indoor experiment on white-breasted nuthatches *Sitta carolinensis*, hoarding intensity peaked in the morning (Waite and Grubb, 1988). This could be species difference, but the conditions in that experiment were different from those in a winter forest. The nuthatches were kept in captivity with food available ad libitum at a temperature of 18.5°C. In autumn when temperatures are mild and food is abundant, the hoarding intensity is highest in the morning also for willow tits (Brodin A, un-

published data; Lahti and Rytkönen, 1996,). The large-scale, long-term hoarding in autumn, however, is different from the daily management of energy supplies in winter (e.g., Brodin and Clark, 1997; Grubb and Pravosudov, 1994).

The environmental stochasticity

This model predicts that hoarders should carry low levels of fat in the morning (<0.2 g) and that this is essential for the pattern of mass gain. Several models (Brodin and Clark, 1997; McNamara et al., 1990) suggest that hoarders should carry enough fat to survive several days. The Brodin and Clark model was designed to examine long-term patterns, and it was not possible to predict precise daily routines from it. McNamara et al. (1990) subdivided each day into half-hour intervals, during which a forager had a low probability of finding food (baseline 0.2). I believe that an arboreal forager experiences the food availability much more predictably. In winter, willow tits have an eating intensity of at least 0.69 items/min (e.g., Brodin et al., 1996), and the birds spend the day moving through a relatively continuous habitat. For short time periods the probability of finding food will then approach 1.0, and, because the winter diet is not very diverse (Haftorn, 1956; Jansson, 1982), the energy gain can be approximated as a rate. There might have been weather changes during the night, but after sampling a few trees in the morning this rate should be predictable to a willow tit. The timeframe for stochastic events should then be adjusted to changes in the environment (e.g., weather) rather than to each single foraging decision.

What is the benefit of short-term hoarding?

According to my model, the main benefit of short-term hoarding is that stored supplies allow hoarders to stay at low body fat levels, thereby avoiding mass-dependent increases in predation risk. Retrieval is nonstochastic, and caches will act as insurance against bad weather and poor foraging success. Under normal weather and foraging conditions, caches are not retrieved. The importance of caches as insurance is also shown by the fact that under the worst possible conditions for hoarding that were modeled, mortality was twice as high for nonhoarders (23%) as for hoarders (11%).

Several authors have discussed short-term hoarding as a separate phenomenon from long-term hoarding. Suggested benefits are to (1) even out fluctuations in the food supply (e.g., Lucas and Walter, 1991; Sherry, 1989; Vander Wall, 1990), (2) secure as much as possible of an ephemeral food source (e.g., Clarkson et al., 1986, Lucas and Walter, 1991, Sherry, 1989), (3) ingest the acquired food when it is optimal (e.g., Lucas and Walter, 1991; McNamara and Houston, 1986; Sherry, 1989), or (4) optimize the daily routines for energy management (McNamara et al., 1990). Of the papers cited above, two are theoretical models that specifically address short-term hoarding: McNamara et al. (1990) and Lucas and Walter (1991). McNamara et al. (1990) predicted a different daily fat gain routine than my model, but found that avoiding mass-dependent costs (metabolism) was important. Lucas and Walter (1991) predicted a daily fat gain pattern more similar to my model but concluded that avoiding mass-dependent predation was less important. They suggest that securing access to food when it is most critical is the main benefit of short-term hoarding. To some degree my model unites these two benefits; hoarding secures access to food when it is most needed (for lean birds in bad weather); thereby they can stay lean and avoid mass-dependent costs. Interestingly, in a model of the long-term use of caches in the acorn woodpecker *Melanerpes formicivorus*, Hitchcock and Houston (1994) reached a

similar conclusion, that caches may be more important as insurance than as energy supply.

APPENDIX A

For caches, y, I use the following:
Energy retrieved from store:

$$\Delta y_{\text{retrieve}} = \begin{cases} \gamma_1 a_C r_A(w_g) & \text{if } y(t,\, d) > \Delta y_{\text{retrieve}} \\ y(t,\, d) & \text{if } y(t,\, d) \leq \Delta y_{\text{retrieve}}, \end{cases}$$

where y are the caches at the beginning of period t on day d, $r_A(w_g)$ is the energy gain from foraging for new food under good weather conditions, and γ_1 is a factor relating the energy reward from retrieval to $r_A(w_g)$. a_C is the proportion of the period spent retrieving. The second line ensures that retrieval will not exceed stores.
Energy stored:

$$\Delta y_{\text{hoarding}} = \gamma_2 a_B r_A(w),$$

where γ_2 is a factor $0 < \gamma_2 < 1$ determining how large a proportion of the encountered food that it is possible to store, a_B is the proportion time spent storing, and r_A is the weather-dependent foraging success (see below). Depending on weather, the stores after one time period are:

$$y'_{\underline{a},w_g} \quad \text{or} \quad y''_{\underline{a},w_b} = y - \Delta y_{\text{retrieve}} + \Delta y_{\text{hoarding}} - \gamma_3 y,$$

where y are the stores at the beginning of the period and γ_3 is the proportion caches forgotten each day.
For fat reserves, x, we have (1) the amount of fat obtained by foraging:

$$\Delta x_{\text{forage}} = a_A[r_A(w)],$$

where $r_A(w)$ is the weather-dependent energy gain when searching for new food and eating it, and a_A is the proportion of the period spent on this activity. (2) The amount of fat obtained by retrieving is:

$$\Delta x_{\text{retrieve}} = \Delta y_{\text{retrieve}}$$

Under baseline assumptions the metabolic cost is linear:

$$C_m = (a_A + a_B + a_C) + (a_A + a_B + a_C)\,C_A\gamma_4 \times \frac{x}{x_{\max}} + a_D C_D,$$

where C_A is the energetic cost of active foraging, a is the allocation of time to the various activities, and γ_4 scales the mass-dependent term. The first term is cost as a function of the amount of active foraging, the second adds linear mass dependence, and the third is the cost of perching. In some runs of the model a quadratic metabolic cost is used:

$$C_q = (a_A + a_B + a_C)\,C_A\gamma_4 \times \left(\frac{x}{x_{\max}}\right)^2 + a_D C_D.$$

Depending on the weather. the fat reserves at the end of the period are:

$$x'_{\underline{a},w_g} \quad \text{or} \quad x''_{\underline{a},w_b} = x + \Delta x_{\text{forage}} + \Delta x_{\text{retrieve}} - C_m,$$

where x is the reserves at the beginning of the period. The baseline case with a linear effect of fat reserves on predation risk, μ_2 is given by:

$$\mu_1 = (a_A\mu_A + a_B\mu_B + a_C\mu_C) + \gamma_5\left(\frac{x}{x_{\max}}\right)(a_A\mu_A + a_B\mu_B + a_C\mu_C),$$

and with the limit under which predation is not mass-dependent introduced:

$$\mu_1 = \begin{cases} a_A\mu_A + a_B\mu_B + a_C\mu_C & \text{if } x < \omega \\ (a_A\mu_A + a_B\mu_B + a_C\mu_C) + \gamma_5\left(\dfrac{x-\omega}{x_{\max}}\right)(a_A\mu_A + a_B\mu_B + a_C\mu_C) \\ \qquad\qquad \text{if } x \geq \omega. \end{cases}$$

Here μ_a is the predation risk for the various activities, and a is the allocation of time to these; x is the fat deposit at the beginning of the period, ω is the limit where predation risk becomes mass dependent and γ_5 is a scaling factor for the mass dependence. A quadratic effect of fat on predation risk is given by:

$$\mu_q = \begin{cases} a_A\mu_A + a_B\mu_B + a_C\mu_C & \text{if } x < \omega \\ (a_A\mu_A + a_B\mu_B + a_C\mu_C) + \gamma_5\left(\dfrac{x-\omega}{x_{\max}}\right)^2(a_A\mu_A + a_B\mu_B + a_C\mu_C) \\ \qquad\qquad \text{if } x \geq \omega; \end{cases}$$

the notation is as above.
Fitness values are known only for discrete points, and for intermediate levels of fat it is interpolated between the nearest higher and lower points. To improve the fitness estimates, death from starvation occurs at fat level $x < 0$ rather than at $x = 0$ as in some earlier models (e.g., Brodin and Clark, 1997; Clark and Ekman, 1995). Otherwise, fitness for fat levels between the two lowest discrete points on the scale, 0 and 1, will be systematically underestimated. As the calculation of fitness propagates backward in time, this will also reduce fitness for higher levels of fat in earlier time periods. Normally distances are good approximations of the influence of the nearest known points. However, if death occurs at $x = 0$, this point will give zero fitness. A bird with fat deposits $0 < x < 1$ will forage intensively to gain fat, so the probability of actually falling to zero may be very small. Linear interpolation means that an individual with, say, 0.1 in fat will get 90% of the fitness value for $x = 0$ and 10% from $x = 1$. This is, of course, a bad estimate of the actual survival probability. With death occurring at $x < 0$, the 0-point can have positive fitness, and interpolation estimates are better. This can be thought of as if the forager at $x = 0$ is on the verge of dying but will live another fraction of time before dying.

APPENDIX B

For values that refer to Brodin and Clark (1997), the details are given in that paper. The rationale for dividing the day into three periods is threefold. First, the field data collected by Lilliendahl (1997a) are presented in this way. Second, it is a convenient time span for stochastic changes in weather, which can change between but not within periods in the model. Third, it saves space in computer memory compared to a model with, say, 200 periods in a day (a reasonable number of foraging decisions for a small bird during a day).
To facilitate comparisons, I show most values as per-day values, even though the basic time unit in the model is one-third of a day. The metabolic cost for a normal night, C_g, is 29.0 kJ (Reinertsen and Haftorn, 1986) and for an unusually cold night, C_b, is $1.2(C_g)$ (Brodin and Clark, 1997). I assume that 1 night of 20 and 1 daytime period of 20 are unusually bad. Then the probability of a normal night, p_{ng}, is 0.95 and the probability of good weather during a daytime period, p_{wg}, is also 0.95.
In willow tits the mean energy turnover in the field is 45 kJ/day (Moreno et al., 1991). In reality some time also needs to be allocated to activities other than foraging (e.g., territory defense and preening). This means that the maximum rate for shorter time periods must be higher than the average over

the whole day. Hence I set the maximum energy gain, r_A, to 70 kJ/day. Under bad weather conditions foraging success, r_A, is 0, but hoarders can still retrieve. The rationale for choosing 0 as baseline value is to ensure that there is a strong effect of daytime stochasticity. I set the maximum possible fat reserves, x_{max}, high (to 200 kJ or 5 g of fat) to ensure that the limit per se will not affect the results. Metabolic costs of activities, C_A, C_B, and C_C, are 12.0 kJ/day and metabolic cost of perching, C_D, is 10.0 kJ/day (Brodin and Clark, 1997). The small difference between active foraging and perching depends on heat production from activity being used for maintaining the body temperature (Pohl and West, 1973, cited in Bruinzeel and Piersma, 1998). The factor γ_4 that scales the mass-dependent energy cost relative to body mass is set to 2. This is calculated from the relation of power being proportional to body mass with $P \propto M^2$ in one individual (e.g., Witter and Cuthill, 1993).

I only address short-term caches in this paper and disregard any loss of caches other than forgetting their location. The reason is that long-term loss in the coniferous forest is only 1% per day (Brodin, 1993). Hoarders forget a constant proportion of caches, γ_1, each day, that I set to 0.10 considering the decay of memory (Brodin and Kunz, 1997; Hitchcock and Sherry, 1990). Depending on the small number of caches made during a winter day (Brodin, 1994; Haftorn, 1956) and the decay of memory, I set the maximum cache size, Y_{max}, to 50 kJ. I assume that 50% of the encountered food is storable, $\gamma_2 = 0.5$, considering the fecal analyses by Jansson (1982) and field observations of foraging tits in winter (Brodin, 1994; Haftorn, 1956). I set the baseline rate of recovering stores, r_C, to $2.0[r_A(w_g)]$, and retrieval is not affected by weather.

For a lean bird not carrying any fat, the predation risks μ_A and μ_B are 0.001/day, and the factor that scales predation risk to body mass, γ_5, is 10. This means that a bird with 1 g of fat reserves will experience a predation risk of 0.008/day. For retrieving, I set the baseline risk, μ_C to 0 because a retrieving bird knows the location of the food item beforehand. A less demanding search for food means better possibilities to scan for predators. To check that this assumption will not affect the results in a noticeable way, I also tested the model with $\mu_C = 0.5\mu_A$, 50% of the risk at foraging. In the model there is a limit under which body mass does not affect predation risk, ω, which under baseline assumptions is 0, meaning that all increases in body mass increases predation risk.

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