

# Plastic daily fattening routines in willow tits

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## Summary

1. Each day small birds must build up sufficient energy reserves, largely fat deposits, for the following night and for the periods when foraging is not possible. The earlier the birds acquire the reserves and the more they carry them, the higher is the insurance value of the reserves. Still, small birds do not forage at maximal capacity during the day and, even at dusk, body reserves are usually below the physiological upper limit. A popular explanation for this is that birds' fatness levels reflect an optimal compromise between starvation risk and risks associated with reserve carrying and acquisition.

2. Theoretical works suggest that uncertain or variable feeding conditions should promote high reserve levels, and that in the daily perspective, feeding should peak in the morning hours. In more favourable conditions, reserve levels should be smaller and the acquisition peak should be delayed towards the end of the day. These predictions were tested by experimentally manipulating winter feeding conditions and monitoring subsequent daily body mass increase in northern population of the willow tit *Parus montanus* (Conrad), a small-sized forest passerine.

3. The birds using feeders appeared heavier than the control birds throughout the day. This contradicts the prevailing theory, but is understandable since the feeding procedure probably not only affected food amount but may also have decreased acquisition costs in terms of predation.

4. Daily mass gain and the gain rates were fairly similar in the food-manipulated and the control birds. However, the mass gain schedules differed between the treatment groups: the food-supplemented birds gained mass at a roughly constant rate while among the control birds the gain rate was higher in the morning than in the afternoon. Probably to avoid associated costs, birds abandon early build-up of reserves if foraging conditions become favourable enough.

*Key-words:* daily mass gain, food predictability, predation, starvation, willow tit, winter survival.

*Journal of Animal Ecology* (2002) **71**, 816–823

## Introduction

Resident birds in high latitudes increase their dawn and dusk masses when the winter approaches (e.g. King 1972; Lehikoinen 1987; Houston & McNamara 1993). 'Winter fattening' is treated as a strategic response to challenges in energy management caused by shortening activity time, harsh weather and non-renewing food sources. Much of the seasonal variation may be explained by increased daily fluctuation in reserves because of increased night-time need of reserves due to longer nights and decreasing temperatures (Lehikoinen 1987).

Fatness levels of birds are in general far below the physiological maximum (e.g. King 1972). This may be due to food constraints, although in general birds do not forage at maximal capacity. Instead, they seem to manage reserves according to varying feeding conditions or energy requirements (e.g. Lima 1986; Ekman & Hake 1990; Bednekoff, Biebach & Krebs 1994; Bednekoff & Krebs 1995; Gosler 1996; Lilliendahl *et al.* 1996). For example, increased foraging uncertainty has been demonstrated to lead to increased levels of external hoards (Hurly 1992; Pravosudov & Grubb 1997) or to internal reserves (Ekman & Hake 1990; Rogers & Smith 1993; Bednekoff *et al.* 1994). Provided that birds have a flexible reserve policy, they also could be able to follow a variety of daily mass gain routines. The critical question is, which kind of gain trajectory should they choose in order to maximize their survival chances?

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Intuitively, if there is considerable uncertainty in feeding success, birds could minimize the risk of energetic shortfall by acquiring reserves for the following night as early as possible. However, an early bird may expose itself for the rest of the day to potential mass-dependent costs of reserves (Blem 1975; Lima 1986; Houston & McNamara 1993; Witter & Cuthill 1993; Houston, Welton & McNamara 1997). High body mass can reduce take-off ability, flight speed or manoeuvrability, which are important for escaping from attacking predators (Witter, Cuthill & Bonser 1994; Metcalfe & Ure 1995; Kullberg, Fransson & Jakobsson 1996; but see, e.g. Veasey, Metcalfe & Houston 1998). Also maintenance and acquisition of the reserves may appear costly in terms of increased energy expenditure and associated use of risky foraging habitats or decreased vigilance (Lima 1986; Ekman 1987). Accordingly, body mass seems to be negatively associated with predation risk in many bird species (Gosler, Greenwood & Perrins 1995; Lilliendahl 1997; Carrascal & Polo 1999; Gentle & Gosler 2001; but see van der Veen 1999). Acquisition costs may have relevance to daily routines if predation risk varies over the course of the day. For example, dawn and dusk may be high-risk periods due to 'a temporal edge effect', i.e. overlapping activity of diurnal and nocturnal predators (e.g. Lima 1988; Lahti, Koivula & Orell 1997).

If the mass-dependent costs are realistic, it could be beneficial to postpone the reserve-build up to the later part of the day. Then, however, birds might jeopardise acquisition of sufficient reserves, especially if foraging interruptions or decrease in foraging efficiency are probable during the day.

McNamara, Houston & Krebs (1990) and McNamara, Houston & Lima (1994) modelled daily foraging routines of small birds and predicted a variety of activity patterns, which in general included an activity peak at the dawn, a slower phase during the day, and another period of intensive feeding near the dusk. The bimodal pattern, commonly observed in nature, represents an optimal compromise between predation and starvation risks when foraging conditions are moderate and foraging may be interrupted during the day (e.g. McNamara *et al.* 1994). In poor foraging conditions and without interruptions McNamara *et al.* (1994) predicted a foraging peak in the early part of the day and a steady decrease after that. After considering digestive constraints, the model of Bednekoff & Houston (1994) also predicted the bimodal feeding activity, and that in uncertain food conditions feeding should be higher towards the start of the day, but in more favourable conditions it should be delayed towards the end of the day. Species that hoard food have the potential to use caches as a short-term alternative to body fat. Among them, the general prediction of the models is that birds should delay reserve build-up until late afternoon (McNamara *et al.* 1990; Brodin 2000). However, if mass-dependent costs emerge only after birds have reached some moderate level of reserves and if cache

retrieval is for some reason inefficient or includes high predation risk, the opposite pattern is expected (Brodin 2000).

Despite extensive theoretical work, potential flexibility with respect to daily reserve build-up routines has received little attention among empiricists. In this paper we intend to partly fill this gap by testing whether free-ranging wintering willow tits *Parus montanus* (Conrad) manage their fat reserves by taking into account the feeding conditions as predicted by the theoretical models (Bednekoff *et al.* 1994; McNamara *et al.* 1994). More specifically, by manipulating food conditions we test the prediction that birds respond to improved feeding conditions by decreasing their body masses. We also test the prediction that rich and invariable food makes the birds postpone reserve build-up until the afternoon while birds with poorer foraging conditions would gain more mass in the morning.

## Methods

### THE STUDY AREA AND THE STUDY OBJECT

The experiment was conducted from 24 November to 12 December 1997 and from 4 to 27 November in 1998. We used free-ranging willow tits living in the study area of about 30 km<sup>2</sup> near Oulu northern Finland (65°N, 25°30'E). The study area is mainly a mosaic of mixed forests of various ages. Scots pine *Pinus sylvestris* (L.), spruce *Picea abies* (L.) and birch *Betula* spp. (L.) are the dominant tree species. Permanent snow cover arrives at the beginning of November and melts in early May. During the winter months temperatures are almost permanently below 0 °C and fall regularly below -20 °C. At the winter solstice the day length is 3.5 h. During the study periods the ground was covered by snow and the mean daily temperature varied between -15 °C and 0.7 °C with the mean of -5 °C. The study area partly borders on an inhabited area. The flocks living in the vicinity of the houses were not sampled to ensure that birds used only natural food before the experiments.

The willow tit is a small (11.5 g) resident forest passerine, and is common in the study area. After initial settlement, which follows natal dispersal in early autumn, birds are site tenacious and usually spend their entire life in the same area. Newly settled juveniles and resident adults form small winter flocks (2–8 individuals) that are relatively coherent and stable in their composition (e.g. Ekman 1979; Koivula & Orell 1988).

Each autumn after flock formation, nearly all the juvenile birds were caught after the flocks were formed. The birds were marked by a numbered aluminium ring and unique combinations of coloured plastic rings. The birds were sexed using sexual dimorphism (wing and tarsus lengths) and the scoring was checked during the next breeding season using sexual differences in behaviour (for details see Koivula & Orell 1988). Birds were aged as adults or first-year juveniles by the method described by Laaksonen & Lehikoinen (1976).

## THE EXPERIMENTAL DESIGN AND BODY MASS MEASUREMENTS

Birds were sampled for the experiment by selectively choosing winter territories from all parts of the study area. The areas were scattered so that there was at least one winter territory between the two focal sites. Although final analyses did not include a block factor for control of nuisance variation, we still attempted to form pairs of sites matched with their habitat characteristics. Within these dyads one site was randomly assigned to the food manipulation treatment and another served as a control. The control birds got no additional food except the ephemeral baits before and during captures. Fresh pork fat and sunflower seeds were provided for the food manipulation group until the start of the last dawn measurements. The possible effect of social dominance on food access was minimized by scattering several feeders over an area of about 0.25 ha. For the same reason feeders were placed in covered sites so that visual contact between the feeding birds would be hindered. During feeding period, the identity of the visitors was regularly controlled in order to ensure that the control birds were not using the feeders and that the birds counted to the treatment group actually were regular visitors.

Feeders were maintained from 1 to 2 weeks before the body mass measurements. Fixed feeding time was not used because measurement days were matched as fully as possible with regard to weather conditions. It is probable that variable treatment time caused no bias since the primary aim was to generate predictable feeding conditions. Therefore, it is the minimum time that is the most critical for successful manipulation. Each day, birds were weighed at one experimental and at one control site. However, owing to practical difficulties, some dyads were weighed within 2 or 3 consecutive days. The design included three repeated mass measurements for each bird within each day (at dawn, noon and dusk). To do this, the birds were trained to respond to a specific signal so that whenever they heard it and were motivated by food, they came to the observer in all parts of their territory (for detailed description of the training procedure see Koivula *et al.* 1995). This allowed large number of birds to be measured within a fixed time period, and even more importantly, there was no need for permanent feeders in the control sites.

Body masses were measured by visual readings from an electronic balance (Sartorius 1002 MP9) with an accuracy of 0.1 g. The balance was used as a feeding tray by placing a small piece of solid pork fat on the weighing plate so that the visits would last long enough to let the balance stabilize. Usually a proper measure was obtained during the first visit, but if possible each bird was weighed several times to minimize measurement errors. Each bird was measured only for 1 day per season.

Each morning the observer arrived at the flock territory 1 h before the sunrise, well before the expected

start of the activity, which during the time of the study took place c. 40 min before the sunrise. The birds were weighed in the sequence they arrived to the balance and exact measurement time was recorded to the nearest minute. At dawn measurements ended when the sun rose. In fact, most of the birds were weighed well before sunrise, but it is not certain that the birds had not fed before the measurements. However, in light of information on dawn activity of the same population (Lahti *et al.* 1997), this should be of minor importance. In the worst case it may generate random variation, but hardly any systematic bias into the data. The mid-day measurements took place within 1 h symmetrically around the noon. In the afternoon the measurements were started 30 min before the sunset. Usually they were completed 30 min after sunset. Afternoon measurements were started relatively early when compared with the average roost-entering time, which in November and December is c. 30 min after the sunset (Lahti *et al.* 1997). Therefore, some birds may have fed after the measurements but apart from random variation, this hardly biased the results.

An individual bird serves as an experimental unit. Our data cover 94 birds (measured in 11 control and 11 experimental sites) of which we managed to weigh 61 at both dawn and dusk and 59 three times within the same day. The control group consisted of 26 birds (15 males, 9 females, 2 unsexed). Exactly half of them were juveniles. The food manipulation group included 33 birds (14 males, 11 females, 8 unsexed) of which 21 were juveniles. Treatment groups were homogeneous with respect to body size (estimated by mean wing and tarsus lengths), median dates of measurements and temperatures of measurement day (test results not shown).

## STATISTICS

Parametric tests were used whenever possible. Before applying them, the normality of the frequency distributions were tested by Kolmogorov–Smirnov statistics. Homogeneities of the subsample and the treatment group variances were tested by Levene's test or in the case of repeated measures ANOVA by Box's test. When applying repeated measures ANOVA and if there was three levels in the within subject factor (time of the day), the assumption of compound symmetry of the variance covariance matrix was checked by Mauchly's test of sphericity (e.g. Potvin, Lechowicz & Tardif 1990). If these assumptions remained violated after transformation attempts, appropriate nonparametric methods were applied. In the case of the repeated-measures ANOVA, Huynh–Feldt corrected significance levels were used when interpreting the results of the univariate tests if the symmetry assumption was violated (Potvin *et al.* 1990).

Day length shortened sharply during the study period and therefore body masses were expected to increase in the course of the experiment. However, day length and variation in ambient temperature were not

**Table 1.** The results of repeated measures ANOVAs explaining the body mass and the mass gain rate by the time of the day (dawn, noon, dusk) and the food treatment (control, food-supplemented)

| Source of variation      | d.f. | Mean square | <i>F</i> | <i>P</i> |
|--------------------------|------|-------------|----------|----------|
| <b>Body mass</b>         |      |             |          |          |
| Within subjects          |      |             |          |          |
| Time of the day          | 2    | 10.072      | 752.757  | 0.000    |
| Time * food manipulation | 2    | 0.036       | 2.699    | 0.072    |
| Error                    | 114  | 0.013       |          |          |
| Between subjects         |      |             |          |          |
| Food manipulation        | 1    | 2.990       | 4.013    | 0.050    |
| Error                    | 57   | 0.745       |          |          |
| <b>Mass gain rate</b>    |      |             |          |          |
| Within subjects          |      |             |          |          |
| Time of the day          | 1    | 39657.194   | 12.334   | 0.001    |
| Time * food manipulation | 1    | 21051.393   | 6.547    | 0.013    |
| Error                    | 57   | 3215.389    |          |          |
| Between subjects         |      |             |          |          |
| Food manipulation        | 1    | 3062.773    | 1.139    | 0.290    |
| Error                    | 57   | 2689.554    |          |          |

expected to cause any systematic bias, because environmental conditions were matched between the treatment groups. Nevertheless, date and temperature were first included as covariates in the ANOVA models. Including them did not change the main results although date turned out to be important when the daily mass gain rates were explained. This association was, however, spurious, because date was strongly associated with day length and therefore was a term of the gain rate. Therefore, and to increase statistical power in testing the original hypotheses, date and temperature were excluded from the final analyses.

## Results

### FOOD SUPPLEMENTATION AND BODY MASS

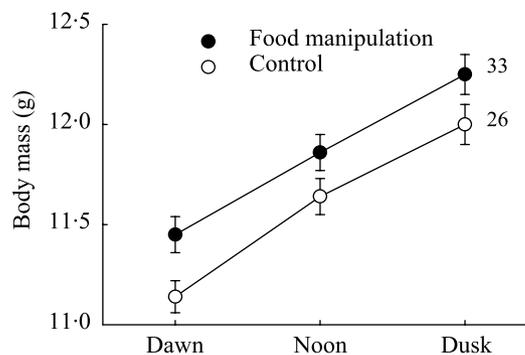
Because of sexual size dimorphism and potential age-dependence of the body mass, we first explained body mass variation simultaneously by food supplementation, sex and age. All these factors were treated as fixed in the repeated-measures ANOVA. As expected, sex appeared a significant factor ( $F_{1,41} = 51.9$ ,  $P < 0.001$ ). Males were heavier throughout the day in both age groups (juvenile, adults) as described by the nonsignificant sex \* age interaction ( $F_{1,41} = 0.234$ ,  $P > 0.1$ ). No mass differences existed between the age groups ( $F_{1,41} = 1.232$ ,  $P > 0.1$ ).

Food-supplemented birds were *c.* 0.3 g heavier than the control birds throughout the day (Fig. 1). This trend applied to both sexes and age groups, since there was no significant interaction between the sex and the treatment or between age and treatment (repeated measures ANOVA; treatment  $F_{1,41} = 7.48$ ,  $P = 0.009$ , sex \* treatment:  $F_{1,41} = 2.925$ ,  $P = 0.095$ , age \* treatment  $F_{1,41} = 2.511$ ,  $P = 0.121$ ). To compare the shapes of daily mass trajectories a second analysis was performed where sex and age were not included as independent between-subjects factors. This was done

in order to increase the resolution of the analysis in observing within-subjects interactions between the repeated (hereafter time) variable and the treatment. In this context it is important to notice that the test above revealed no time \* age ( $F_{2,82} = 1.581$ ,  $P = 0.212$ ) or time \* sex ( $F_{2,82} = 1.373$ ,  $P = 0.259$ ) interaction among the within-subjects effects. After the exclusion of the sex and age, the treatment effect still appeared, but the within-subjects interaction between the food treatment and the time of the day remained just beyond the level of significance (Table 1). In a strict sense this suggests parallel mass gain trajectories in the food manipulated and the control birds (Fig. 1).

### DAILY MASS INCREASE

The daily mass gain varied between 0.4 and 1.5 g with the mean of 0.84 g (SE = 0.025,  $n = 61$ ), which represents 8.1% rise to the mass at dawn (11.31 g, SE = 0.064 g,  $n = 61$ ). The mean mass gain rate was 141 mg h<sup>-1</sup> (range: 60–265 mg h<sup>-1</sup>, SE = 4.8,  $n = 60$ ). There was no significant correlation between the date and the daily mass increase (two-tailed Spearman rank



**Fig. 1.** Mean body masses (with SE bars) of the food-supplemented and the control birds at dawn, at noon and at dusk. Sample sizes are given beside the error bars.

**Table 2.** Mean daily mass gain and mean mass gain rate ( $\pm$  SE) in the food-supplemented and the control birds (numbers of individuals in parentheses). Treatment effect on the mass gain tested by two-tailed Mann–Whitney  $U$ -test. Gain rates and activity times tested by two-tailed  $t$ -test

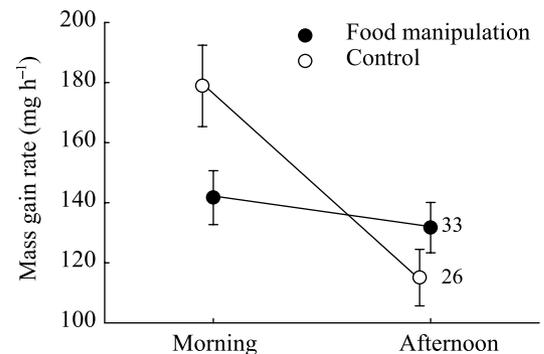
|                                 | Control               | Manipulation          | $P$   |
|---------------------------------|-----------------------|-----------------------|-------|
| Mass gain (g)                   | 0.89 $\pm$ 0.035 (28) | 0.80 $\pm$ 0.033 (33) | 0.155 |
| Activity time (min)             | 364 $\pm$ 8.7 (27)    | 352 $\pm$ 7.0 (33)    | 0.335 |
| Gain rate (mg h <sup>-1</sup> ) | 145.9 $\pm$ 6.86 (27) | 137 $\pm$ 6.14 (33)   | 0.334 |

correlation  $r_s = -0.10$ ,  $n = 61$ ,  $P = 0.939$ ). The daily mass gain rate, however, was positively correlated with the date (two-tailed Pearson correlation  $r = 0.424$ , d.f. = 60,  $P = 0.001$ ). Therefore, in the scale of c. 40 days study period, birds kept their daily mass gain fairly constant but increased their accumulation rate when the day length shortened. The daily mass gain and the gain rates from dawn to dusk were fairly similar in the food-manipulated and the control birds (Table 2). This implies that despite of the difference in the general body mass levels, the treatment groups followed roughly similar daily mass variation patterns.

Birds gained more mass during the morning hours than in the afternoon (0.45  $\pm$  0.020 g vs. 0.38  $\pm$  0.021 g, two-tailed Wilcoxon signed ranks test:  $Z = -2.00$ ,  $P = 0.045$ ). This was not due to a parallel asymmetry in the activity time. In fact, afternoon periods tended to be longer than morning periods (178  $\pm$  3.9 min vs. 182  $\pm$  3.6 min; two-tailed Wilcoxon signed ranks test  $Z = -1.861$ ,  $P = 0.063$ ). Therefore, the mass gain rate also appeared to be higher during the morning hours than the afternoon (158  $\pm$  8.1 mg h<sup>-1</sup> vs. 124  $\pm$  6.29 mg h<sup>-1</sup>; two-tailed paired  $t$ -test  $t_{58} = 3.09$ ,  $P = 0.003$ ). When the treatment groups were analysed separately, the above pattern emerged in the control birds (mass gain:  $Z = 2.351$ ,  $P = 0.019$ , gain rate:  $t_{25} = 3.566$ ,  $P = 0.001$ ), but not in the food-supplemented birds (mass gain:  $Z = 0.310$ ,  $P = 0.756$ ; gain rate:  $t_{32} = 0.82$ ,  $P = 0.419$ ). These results suggest that daily trajectories were different in the treatment groups. To check this, gain rates were analysed by repeated measures ANOVA first including also sex and age in the model. These were, however, dropped from the final analysis since none of them contributed significantly to the gain rate variation. There appeared a significant within-subjects interaction between the treatment and the time of the day (Table 1). This means that the food-supplemented birds gained mass at roughly similar rates in the morning and in the afternoon, while the control birds' gain rate was higher in the morning (Fig. 2). The treatment effect was, however, not significant, which confirmed that food supplementation did not change the gain rate in the scale of the whole activity period. (Table 1).

## Discussion

The birds using feeders had higher dawn masses than the control birds. Food supplementation had no effect

**Fig. 2.** Mean gain rates (with SE bars) of the repeatedly measured food-supplemented and control birds in the morning and in the afternoon. Sample sizes are given beside the error bars.

on daily mass gain and as a result fed birds were heavier in the dusk, too. These observations contrast with the pattern predicted and hence, do not support the prevailing theory, which suggests a decrease in reserves when food becomes abundant, less variable or predictable (e.g. McNamara & Houston 1990; Bednekoff & Houston 1994; Clark & Ekman 1995). Neither are the results in line with the empirical knowledge including reports of positive associations between reserve levels and uncertainty in energy consumption (night-time temperatures) or feeding conditions (e.g. Ekman & Hake 1990; Ekman & Lilliendahl 1993; Bednekoff *et al.* 1994; Witter & Swaddle 1995; Gosler 1996; but see Koivula *et al.* 1995; Verhulst & Hogstad 1996; Pravosudov & Lucas 2000).

The pattern observed is most easily explained by the absence of food constraints when the feeders were available. However, the control birds gained mass at the higher rate in the morning than in the afternoon, implying that unless there was daily variation in feeding conditions, which is questionable, birds were hardly constrained by food availability or foraging conditions in general. An alternative explanation is that the feeders not only decreased starvation risk, but also had marked decreasing effect on mass-dependent costs of fat and birds' response was to increase reserve levels. First, feeders may provide safe feeding conditions. For example, birds using feeders may have been able to fill their gut rapidly, and thereby could shorten the time they are exposed to predation, or fed birds may have been able to devote more time to predator surveillance (Hogstad 1988). Houston & McNamara (1993) also

suggested that if food availability increases sufficiently, not only starvation but also predation risk decrease. In fact, theoretical work suggests that the main benefit of increase in food availability in terms of survival can be the decrease of predation (Houston & McNamara 1993). Accordingly, Jansson, Ekman & von Brömssen (1981) showed that extra food improved winter survival among willow and crested tits *Parus cristatus* (L.) which was at least partly due to lower predation among fed birds (see also Lahti *et al.* 1998). Second, fed birds may have been able to decrease their flying activity and hence energetic costs of carrying fat load. It is also possible that decrease in flying activity leads to body mass increase through increase in muscle mass. Swaddle & Biewener (2000) observed this kind of strategic response in starling *Sturnus vulgaris* (L.) musculature when manipulating birds' flight exercise.

Food-supplemented and naturally feeding birds did not differ in their overall mass gain or mass gain rates from dawn to dusk. This implies negligible differences in night-time energy consumption between the treatment groups. The pattern is analogous to the results of Ekman & Lilliendahl (1993) who observed no differences in daily mass gain between the social classes of willow tits that differed with respect to food access. The response observed is interesting, because one might expect that in good foraging conditions birds would gather excess fuel to avoid need for extensive night-time energy saving and associated costs. That these costs exist is probable, because there is no other apparent reason why birds abandon certain behaviours that have an energy-saving function when conditions develop that are energetically more favourable. For example, birds use night-time hypothermia only in energetically demanding conditions and it is suggested that a negative association between body temperature and nocturnal predation risk explains the pattern (Reinertsen & Haftorn 1984; Haftorn 1992; Bednekoff *et al.* 1994).

Although we did not find any treatment effect on the total daily mass gain, there was a clear difference in daily gain trajectories between the treatment groups. The food-supplemented birds seemed to gain mass at a relatively constant rate while in natural feeding conditions birds gained significantly more mass and had a higher gain rate in the morning hours than in the afternoon. The difference in the gain patterns between the treatment groups fits well with the predictions deduced from models of McNamara *et al.* (1994) and Bednekoff & Houston (1994), i.e. that poor or uncertain foraging conditions should promote reserve build-up early in the day. However, it must be highlighted that in contrast to our results, number of earlier studies have shown birds to be quite conservative in their mass gain patterns. For example, Pravosudov & Lucas (2000) found no change in fairly constant daily mass gain of Carolina chickadees *Poecile carolinensis* (Audubon), when food abundance and variance was experimentally altered. Ekman & Lilliendahl (1993) found that juvenile willow tit males tended to gain mass at a higher rate

before noon than after it, but otherwise no clear association between timing of reserve acquisition and social rank existed as would be expected if dominance equals resource access and predictability (see also Pravosudov & Lucas 2000; Broggi & Brotons 2001). Similarly, Cresswell (1998) found no seasonality in daily mass gain pattern of blackbirds *Turdus merula* (L.), which gained most mass during the morning regardless of the phase of the winter.

Neither group in our experiment showed an afternoon-biased mass gain pattern, although in the presence of mass-dependent costs, the willow tit and other food-hoarding species are expected to increase consumption of food items towards afternoon, while hoarding should be preferred in the morning (McNamara *et al.* 1990; Hurly 1992). Provided that consumption rate and mass gain are positively correlated, our results do not support these suggestions. One probable explanation is that in the theoretical scenario of McNamara *et al.* (1990) external caches and fat reserves were assumed to be short-term alternatives in energy management. This may not be realistic in northern willow tits, especially at the time the study was conducted. Willow tits apparently hoard food for insurance in a longer time perspective than a day and, in fact, abandon intensive hoarding when the winter comes (Haftorn 1956; Brodin & Ekman 1994; Brodin 1994; Brodin 2000). In this light, it is interesting that the fairly constant trajectory observed in fed birds resembles the one predicted for nonhoarders by McNamara *et al.* (1990), which was also found (Lilliendahl *et al.* 1996) for the nonhoarding great tit *P. major* L.

Another explanation for the absence of afternoon bias is that mass-dependent costs associated with changes in flight ability are not as important as has been suspected. In fact, Kullberg (1998) found no mass-dependent effects on take-off ability in willow tits when their mass varied within the normal daily range. However, the laws of physics make the costs inevitable. As a response to this, Brodin (2001) suggested that birds might be able to compensate the effect of increasing load by a parallel gain in their flight muscle. Consequently, mass-dependent costs may become significant only after the reserves reach some threshold level above which compensation is not possible or becomes expensive due to associated (e.g. metabolic) costs (Brodin 2000, 2001). Above the threshold that can be near the normal reserve levels in the dusk, birds are expected to switch to hoarding. In such circumstances, and especially if hoarding is ineffective or costly, hoarding species are expected to show a morning-biased gain pattern (Brodin 2000), which clearly appeared in our data among naturally feeding birds.

As far as the *a priori* predictions are concerned, the interpretation of the two main results, the effect of extra food on overall reserve levels as well as its effect on daily mass gain pattern, is straightforward. However, construction of a comprehensive *ad hoc* explanation for both the main results requires an additional

element into the argument above. If the birds using feeders experienced safe feeding conditions as explained, they seemed to respond differently with regard to the daily trajectories. If extra food decreased predation risk as presumed, then why did the fed birds postpone their reserve acquisition instead of choosing an even more morning-biased schedule than the control birds? One solution for the inconsistency could be that predation risk varies during the day and food supplementation decreased predation risk especially in the late afternoon. Twilight might well represent a risky period, because the most serious predators for boreal tits are nocturnal (small mustelids and owls). Lahti *et al.* (1997) found that food-supplemented willow tits shortened their dusk activity. At dawn Lahti *et al.* (1997) found no such effect. According to Haftorn (1989), Norwegian (65°N) *Parus* species seem to be more reluctant to extend their activity after the sunset than before the sunrise throughout the winter. These findings imply that willow tits tend to avoid dusk feeding and peak in predation risk is one potential cause for it, especially if mass-dependent effects stress the costs of late foraging. Therefore, it can be hypothesized that in addition to predation starvation trade-off, there can also be a trade-off between avoidance of daytime and twilight predation. Morning-biased reserve acquisition could reflect not only importance of starvation avoidance, but also relative importance of acquisition costs in the dusk. Fed birds may have found both types of predation risk lower and therefore increased their general reserve levels as well as postponed their mass gain towards the dusk. High acquisition costs in the dusk could also be the factor that corrupts the applicability of afternoon-biased reserve gain tactics, i.e. that food caches are build in the morning and retrieved for fat reserve build-up in the afternoon (see Brodin 2000).

### Acknowledgements

We thank Petri Kärkkäinen and Seppo Rytönen for field assistance. The study was financially supported by the Research Council for Biosciences and Environment of the Academy of Finland and the Thule Institute of the University of Oulu.

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Received 1 February 2002; revision received 14 May 2002