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Daily body mass regulation in dominance-structured coal tit (*Parus ater*) flocks in response to variable food access: a laboratory study

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In a dominance-structured flock, social status may determine priority of access to food. Birds of low social status may perceive present and future access to food as less predictable, and so have a higher risk of starvation, than birds of high social rank. Theoretical models predict that subordinate birds should carry larger fat reserves and incur higher mass-dependent costs than dominants. However, empirical tests of the assumptions of these models are still scarce and controversial. We investigated the effect of dominance rank on daily mass gain under conditions of fluctuating food availability in a laboratory experiment using four flocks of four coal tits (*Parus ater*) each. The same amount of food was delivered in two treatments, but in one treatment the food was offered at a constant rate between days (fixed treatment), while in the other treatment the daily food supply varied in an unpredictable sequence between days (variable treatment). All birds showed greater variance in body mass in the variable treatment than in the fixed treatment. Body mass within birds showed the same variability at dawn than at dusk in the fixed treatment, but less variability at dawn than at dusk in the variable treatment. This may be a mechanism to reduce the immediate risk of starvation at the beginning of the day, when fat reserves are at their lowest and the aggression between flock members when feeding highest. Subordinate birds were excluded from the feeders by dominants more often in the early morning than in the rest of the day, and they showed more variability in daily mass gain and body mass at dawn than dominant birds. These results support the hypothesis that subordinate birds have a reduced probability of surviving when food availability changes unexpectedly compared to dominants. *Key words:* body mass regulation, coal tits, food access, social rank, starvation risk, *Parus ater*. *[Behav Ecol 13:696–704 (2002)]*

In temperate habitats, small resident birds experience harsh environmental conditions during winter of a reduced and unpredictable food supply and high thermoregulation costs (Walsberg, 1983). To minimize the seasonal increase in the risk of starvation caused by long, cold nights and limited or unpredictable food intake, small birds increase their level of body reserves (Gosler, 1996; Haftorn, 1989; Lehikoinen, 1987; Pravosudov and Grubb, 1997; Rogers and Rogers, 1990). However, there are also costs associated with acquiring and maintaining higher energetic reserves (e.g., mass-dependent predation and mass-dependent energetic costs of locomotion; see Houston and McNamara, 1993; Houston et al., 1997; Metcalfe and Ure, 1995; Witter and Cuthill, 1993). Therefore, birds generally maintain levels of fat reserves below the maximum possible (Blem, 1976; see review in Witter and Cuthill, 1993).

Many birds resident at high latitudes forage in social groups during winter, and often the dominance hierarchy determines the priority of food access to the individual members (e.g., Ficken et al., 1990; Matthysen, 1990). One of the most important advantages of living in a social group for a small bird is an increased likelihood of finding and capturing food (Beletsky and Orians, 1989, 1991). To be weighed against this benefit, there are the costs of living in a social group such as increased competition for food, mainly when food availability is drastically reduced. Therefore, the body reserves of birds living in a group should reflect a compromise between these costs and benefits.

In a stochastic environment, subordinate members might have limited access to the resources when dominant members are present (e.g., Ekman et al., 1981; Lens et al., 1994; Morse, 1974). As a consequence of resource predictability being dependent on social status, subordinate birds should perceive a higher risk of starvation than dominant members. The theoretical models therefore predict that dominance rank in a flock might affect fat levels (i.e., the lower the rank, the higher the level of fat reserves; Clark and Ekman, 1995; McNamara and Houston, 1987, 1990), and observational data seem to support this prediction (Ekman and Lilliendahl, 1993; Gosler, 1996; Witter and Swaddle, 1997; but see Nolan and Ketterson, 1983).

Another interesting question is the extent to which the unpredictability of foraging conditions may affect the variability in body reserves of individual birds. Unpredictability in foraging success during winter may produce increased variability in the level of body reserves at the end of the day (Hurly, 1992) but also at the beginning of the day. Under such conditions, on an unfavorable day, birds might fail to achieve sufficient energetic reserves and would starve (Hurly, 1992; Stephens and Charnov, 1982). To cope with this unpredictability in food supply, birds may increase their body reserves (Bednekoff and Krebs, 1995; Ekman and Lilliendahl, 1993; Pravosudov and Grubb, 1997) and start their foraging activity as soon as possible in the day (Fitzpatrick, 1997; Gosler, 1996). In addition, variation in body mass should be lower in the morning than at other times of day to mitigate the high threat of starvation at the beginning of the day. Evening body mass

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and weight loss over the subsequent night are positively associated (Bednekoff and Krebs, 1994; Haftorn, 1992). This suggests a possible mechanism to maintain more stable levels of minimum body reserves at the start of the day.

Aggressiveness between flock members is likely to increase when food resources are scarce, especially at the start of the foraging period. Dominant birds may increase their intake by displacing subordinate birds from the best foraging sites. Therefore, subordinate birds should be more prone to lose body mass and to suffer an energetic shortfall than dominants (Caraco et al., 1989; Clark and Ekman, 1995), leading to greater variability in body reserves in subordinates.

Members of the *Parus* genus of tits form flocks with a stable dominance rank, with males dominant over females and adults dominant over younger individuals (Ekman, 1979, 1987; Hogstad, 1988, 1989; Lens et al., 1994). In this study we examined the above hypotheses in relation to social rank, variability of body reserves, and unpredictability of food in a laboratory experiment with flocks of coal tits (*Parus ater*). The relationship between dominance rank and body reserves (mean and variability) was tested by manipulating the predictability of the food supply. The same total amount of food was delivered either at a constant rate within days (fixed treatment), or in an unpredictable sequence among days (variable treatment). High variability in daily food availability among days should induce high variability in body mass at dawn and dusk. This variability should be larger in subordinates than in dominants. Moreover, competition for food should be most intense at dawn and in the variable treatment.

MATERIALS AND METHODS

Subjects, apparatus, and rearing conditions

Between January and February 1997, we captured 16 adult coal tits (*Parus ater*) in ''El Ventorrillo'' field station (4°1′ W, 40°45′ N; 1500 m above sea level; Sierra de Guadarrama, Spain). Birds were caught and experiments were conducted under local license. We color-ringed birds and randomly allocated them into four flocks of four birds each. A flock of four birds is the most common size in *Parus* during winter (Ekman, 1989; Matthysen, 1990). Flocks were housed indoors in four cages (40 × 30 × 100 cm, height × width × length) at 18 ± 2°C on an 8.5 h light:15.5 h dark photoperiod. The changes between light and dark were gradual and lasted 15 min. In the last 15 min of the day, all cages were cleaned and spilled food recovered. Caching attempts were occasionally observed, but they were unsuccessful because cages did not offer suitable sites to build food caches.

Each cage had four perches and two drinking bottles. There was an operand panel in the center of the back wall of each cage with a colored light, 2 cm to the side of a central food hopper. Colored light was used as the discriminate stimulus indicating the availability of the next food reward. The food hopper had a pecking key attached, and it was connected to a pellet dispenser (Campden Instruments, Loughborough, UK) filled with dry kitten cookies (IAMS Company, Dayton, Ohio, USA) ground and sieved to an even size. One unit of food averaged 0.04 g and took 1 s to deliver. An Acorn RiscPC-600 microcomputer running Arachnid experimental control language (CeNeS Cognition, 1990) controlled the stimulus events and response contingencies and also recorded part of the data. The size of the food hopper allowed two birds to forage together, but most of the time (> 90% of feeds) only a single bird fed at a time.

After a week of acclimation to the cages (when food was provided by a separate feeder), birds were induced to peck the response keys by a standard autoshaping procedure. Coal tits initially experienced the delivery of standard rewards (0.16 g; 4 units of food) preceded by 8 s of a light near to the center key, with an intertrial interval (ITI) of 262 s. They were then gradually shifted to an operant schedule where rewards were delivered conditional on key pecking at the central key. In each trial the light near the center key was on for 8 s, and pecking would cause the light to go off and the delivery of a standard reward. If no peck occurred in the 8-s interval, the light was turned off and the ITI started. Therefore, birds had a chance to feed every 270 s during 8.5 h. This schedule allowed the flock to obtain a theoretical maximum of 18.1 g of food per day (i.e., 113 trials × 4 units × 0.04 g). This amount was twice the mean daily intake per bird measured on other coal tit flocks living with food ad libitum (2.3 ± 0.1 g per bird and day; $n = 4$ birds) and kept with the same light:dark cycle in the same cages and conditions. Flocks were kept on this training schedule for 2 weeks.

Treatments

After the 2-week training period, two 18-day treatments were applied: a fixed treatment that was identical to the training schedule (i.e., all rewards with medium food availability [M] of 4 units of food; less than 18.1 g per flock per day), and a variable treatment that was set by days with low or high food availability. On days of low food availability the computer was programmed to deliver 2 units of food each time (0.08 g; i.e., up to 9.0 g per flock per day). On days of high food availability 6 units of food were delivered each time (0.24 g; i.e., up to 27.2 g per flock per day). Therefore, low food days were the only ones where birds were subjected to a strict diet, where the maximum feeding rate would equal the normal daily requirements of the flock. Days of high food availability (H) were alternated with days of low food availability (L) in an unpredictable fixed sequence: HLHHLHHLHHLLHHLLHL. This sequence showed variability in pairs and triads of days without including three H or L consecutive days. We prevented 3 consecutive days of low food availability to avoid high starvation risk in subordinate birds. Two flocks experienced the fixed treatment first, and the other two started with the variable treatment, and the treatments were then reversed. We used only data of the last 14 days of each treatment in the analyses.

Feeding activity of small birds can be influenced by the level of predation risk (Lima, 1998). Thus, daily body mass can be affected by food availability, but it is also a consequence of the predation risk (Cresswell, 1998; Gosler et al., 1995). The perceived risk of predation was the same in both treatments because the daily routines when recapturing and weighting the birds was identical in both treatments. Hence, we did not consider the predation risk as a factor of daily body mass regulation in the present study.

Data collection

We monitored the body weight of the birds during the experiment. This was particularly important in the variable treatment because we were testing for a possible larger variability in body mass in subordinate birds than in dominants, while avoiding a weight loss beyond the boundaries of natural variation in the wild. Every lights-on and lights-off, we caught the birds by hand and weighed them, within a plastic box, by using an electronic digital balance (precision 0.01 g). Birds were not able to obtain food in the dark period (i.e., between lights-off and lights-on in the next day). Less than 12 min were necessary to weigh all birds. The difference between lights-off and lights-on weights was assumed to represent an increase in body reserves (Blem, 1990; Webster, 1989).

Table 1
Mean body masses by treatment and time of day

		Body mass at dawn, g (SE)		Body mass at dusk, g (SE)	
Flock	Bird	Fixed	Variable	Fixed	Variable
	1	9.32 (0.04)	9.01 (0.07)	10.37 (0.04)	10.27 (0.06)
1	2	9.34 (0.07)	9.72 (0.07)	10.23 (0.08)	10.81 (0.07)
	3	9.85 (0.04)	9.83 (0.09)	10.75 (0.03)	10.87 (0.10)
	4	9.69 (0.03)	9.57 (0.09)	10.61 (0.03)	10.57 (0.09)
	5	9.90 (0.02)	9.70 (0.02)	11.07 (0.04)	10.80 (0.01)
2	6	9.16 (0.04)	9.31 (0.02)	10.14 (0.06)	10.31 (0.05)
	7	8.91 (0.04)	8.59 (0.02)	9.99 (0.06)	9.64 (0.03)
	8	8.30 (0.02)	8.24 (0.02)	9.18 (0.02)	9.14 (0.02)
	9	10.14 (0.02)	9.89 (0.03)	11.30 (0.02)	11.01 (0.04)
3	10	9.44 (0.03)	9.18 (0.05)	10.51 (0.03)	10.17 (0.09)
	11	8.90 (0.03)	8.79 (0.03)	9.97 (0.03)	9.81 (0.04)
	12	9.02 (0.01)	8.89 (0.05)	10.10 (0.02)	9.93 (0.11)
	13	10.42 (0.03)	9.98 (0.08)	11.45 (0.04)	11.09 (0.11)
4	14	9.70 (0.03)	9.74 (0.06)	10.72 (0.04)	10.75 (0.10)
	15	8.35 (0.05)	7.94 (0.08)	9.19 (0.06)	8.77 (0.09)
	16	9.63 (0.04)	9.34 (0.10)	10.40 (0.04)	10.20 (0.13)
	All	9.40 (0.04)	9.23 (0.06)	10.37 (0.04)	10.26 (0.07)

In the fixed treatment all days had medium food availability. In the variable treatment, days with high and low food availability were combined (see Methods for details). Subjects are arranged by dominance rank (numbers 1, 5, 9, and 13 are the most dominant birds).

We measured social ranks within a flock by recording the outcome of paired aggressive encounters among all flock members (i.e., displacements from the food hopper, chases, and aggressive interactions). Because the birds were color banded, we were able to assign the winner and loser in each aggressive encounter. All data were recorded through a one-way window. We recorded the number of aggressive interactions in a flock during the first and last three food offers of each day (i.e., 13.5 minutes at both ends of the foraging period). Therefore, 7 days of data on social ranks were recorded from each flock (giving total sample sizes of 149, 137, 184 and 235 paired encounters for the 4 flocks, respectively). The hierarchy in each flock was calculated as the proportion of aggressive encounters won by each bird (Hogstad, 1987). Aggression rate in a flock was expressed as number of aggressive interactions per minute.

Use of the food hopper by the birds was also recorded during the first and last three food offers of the feeding period. We recorded the percentage of time that the food hopper was used by one bird, by more than one bird, or vacant. We also recorded the identity of the foraging bird and its proportion of time using the hopper. A standard reward was consumed in less than 30 s. Therefore, we only timed the use of the operand feeder in the first 30 s after each of the three rewards was delivered. A total of 224 observations of focal birds occupying the feeder were obtained.

Statistical analyses

We used data on the last 14 days of each treatment and time of day to obtain the mean body mass at dawn and at dusk, their respective coefficient of variation (CV), and the mean daily mass gain for each bird. To study the effect of treatment on mean body mass of the birds, on their mean daily gain in body mass, and on the CV of these variables, repeated-measures ANOVA analyses were used. Individual birds cannot be treated as fully independent statistical units in this experiment because they were arranged in four cages of four birds each. To overcome this problem we included each flock in the ANOVA models as a between-subject blocking factor. With this procedure the repeated-measures effects were estimated controlling for the main effect of the differences between the flocks. We used differences in CV of the mean body mass between birds as a measurement of differences in body mass stability arising from manipulations of the predictability of the food supply. The effect of food availability (i.e., medium food availability in the fixed treatment and low and high food availability in the variable treatment) on mean daily gain in body mass was analyzed with repeated-measures ANOVA with the flock as a blocking factor and planned post-hoc comparisons.

We analyzed the effect of food availability on the percentage of time at the food hopper and the rate of aggressive encounters within flocks with repeated-measures ANOVA models and planned comparisons. The effect of dominance rank on daily body mass gain and food access was analyzed by combining the results of simple ANOVA analyses and planned comparisons on the data obtained within each flock, using the combined probabilities test (Sokal and Rohlf, 1995). We used a chi-square test to combine four independent ANOVA tests [$\chi^2 = -2\,\Sigma_i \ln(p_i)$, df = 8; see Sokal and Rohlf, 1995]. This test was also used to look for intraindividual differences in diurnal mass gain by combining the results of ANCOVA analyses from each flock, with nocturnal mass lost, body mass at dawn, and day of treatment defined as covariate, and treatment as a fixed factor.

All percentages were arcsine-root transformed before analyses, and aggression rate was Box-Cox transformed. We considered probabilities $< 5\%$ significant. All tests were two-tailed.

RESULTS

Body mass by treatment

Mean body mass at dawn in the fixed treatment was only 0.17 g larger than in the variable treatment (two-way repeated measures ANOVA, with the flock as a between-subject blocking factor, $F_{1,12} = 7.58$, $p = .017$; Table 1). Mean body mass at dusk was not significantly different between treatments (two-way repeated measures ANOVA, $F_{1,12} = 4.12$, $p = .065$; Table 1). Therefore, differences in mean diurnal mass gain between treatments, although significant, were very low (0.99 vs. 1.03

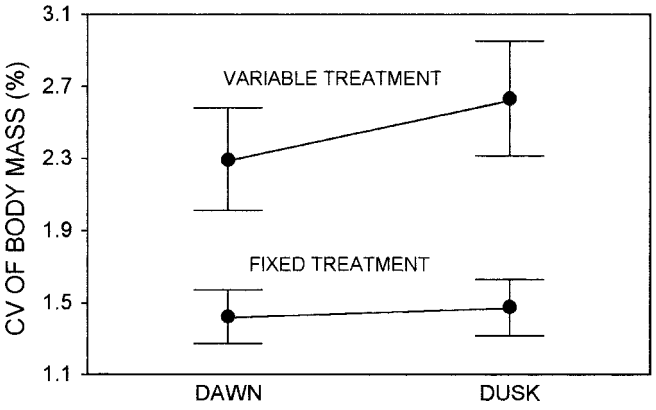

Figure 1
Coefficient of variation (CV) in body mass at dawn and dusk in the fixed and variable treatments. Data points are the mean of the CV in body mass (± 1 SE) of 16 coal tits across 14 days in each treatment.

g comparing fixed vs. variable treatment: two-way repeated measures ANOVA, $F_{1,12} = 8.14$, $p = .015$). The flock (blocking factor) was not a significant effect in these analyses ($F_{3,12} < 1.30$, $p > .32$).

The CV of body mass over the last 14 days of the variable treatment was significantly larger than the CV measured over the same days of the fixed treatment (2.47 vs. 1.45% comparing variable vs. fixed treatments; three-way double-repeated measures ANCOVA of the CV of body mass: dawn vs. dusk and fixed treatment vs. variable, $F_{1,12} = 21.26$, $p < .01$; see Figure 1). Body mass was more variable at the end of the foraging period than at the start of the day ($F_{1,12} = 19.55$, $p < .01$). In the variable treatment the difference in CV of body mass between dawn and dusk was larger than in the fixed treatment (interaction between treatment and period of day, $F_{1,12} = 4.79$, $p < .05$). The CV of daily mass gain in days with variable food availability was much larger than the CV measured in days with constant food availability (33.2 vs. 10.9%; two-way repeated measures ANCOVA, $F_{1,12} = 86.1$, $p < .01$). These effects controlled for significant differences between flocks in the CV of body mass and diurnal mass gain (blocking factor effect of flock identity on body mass: $F_{3,12} = 4.79$, $p < .01$; diurnal body mass: $F_{3,12} = 10.63$, $p < .01$).

In summary, greater unpredictability of food supply between days increased the variability in body mass and diurnal mass gain but provoked little change in the mean levels of these variables. The increased variability of body mass of coal tits in response to variable food availability between days was greater at dusk than at dawn.

Body mass by food availability

The food availability each day determined the mean percentage of body mass that coal tits gained each day (two-way repeated measures ANOVA and planned comparison high > fixed > low food availability; 13.95 vs. 10.62 vs. 8.43% in the high, fixed, and low food availability respectively, $F_{1,12} = 166.55$, $p < .01$). The mean daily gain of body mass was not different between flocks ($F_{3,12} < 1.6$, $p > .24$).

In the variable treatment there were pairs of consecutive days of either low or high food availability. The diurnal body mass gain was different on the first day compared to the second day. When both days had a low food availability, the birds gained less mass on the first day compared to the second (9.48 vs. 9.63%; two-way repeated measures ANOVA, $F_{1,12} = 39.26$, $p < .01$). In contrast, when both days had a high food availability, the body mass gained on the first day was larger than that on the second day (15.07 vs. 12.98%; $F_{1,12} = 112.12$, $p < .01$).

Intraindividual differences in diurnal mass gain, nocturnal mass lost, and body mass at dawn

Differences between birds and differences in daily food availability together accounted for 32.5% of the variance in diurnal mass gain (two-way ANCOVA analyses in each flock, with bird as random factor, the level of food availability as fixed factor, and body mass at dawn, body mass lost in the previous night, and day of treatment as covariates; individual effect: $R^2 = 10.19\%$, $\chi^2 = 62.89$, df = 8, $p < .001$; food availability effect: $R^2 = 22.30\%$, $\chi^2 = 45.63$, df = 8, $p < .001$; combined probability test). Body mass lost over the previous night and body mass at dawn together explained a further 17.3% of intraindividual differences in diurnal body mass gain (covariate effect: $R^2 = 18.76\%$, $\chi^2 > 80$, df = 8, $p < .01$). The daily gain in body mass was larger on days when the body mass at dawn was smaller ($R^2 = 12.39\%$, $\beta = -0.40$, $\chi^2 = 69.12$, df = 8, $p < .001$) and when the overnight loss in body mass had been greater ($R^2 = 4.91\%$, $\beta = 0.09$, $\chi^2 = 28.14$, df = 8, $p < .001$).

However, these relationships between diurnal mass gain and both the body mass at dawn and the overnight mass loss varied according to the level of food availability (two-way ANCOVA analyses in each flock; food availability × covariates; $\chi^2 = 68.27$, df = 8, $p < .001$; combined probability test). This was the result of a significant effect of covariate variables (i.e., body mass at dawn and overnight mass loss) on the diurnal gain of body mass in days of high or medium food availability, but not on days of low food availability (post-hoc one-way ANCOVA analyses in each flock combined in a single test; high or medium food availability: $\beta = -0.47$, $\chi^2 > 80.0$, df = 8, $p < .001$; low food availability: $\beta = -0.11$, $\chi^2 > 15.0$, df = 8, $p = .06$). In summary, coal tits gained more body mass on days that they began with a low body mass, but this pattern only occurred on days when food was sufficiently plentiful (i.e., high or medium food availability).

Interindividual differences in daily mass gain by dominance hierarchy

Position in the dominance hierarchy and the flock in which a bird was found explained 73.7% of interindividual differences in the percentage of daily mass gain (multiple regression analyses within food availability, with flock as three dummies variables and the percentage of aggressive encounters gained as the covariate variable: $\chi^2 = 45.79$, df = 6, $p < .001$; combined probability test). Both effects accounted for a significant portion of the variance (flock: $R^2 = 63.2\%$, $\chi^2 = 35.46$, df = 6, $p < .001$; dominance hierarchy: $\chi^2 = 18.15$, df = 6, $p = .006$; combined probability test). Coal tits that won the highest proportion of aggressive encounters gained more weight each day, and this relationship was strongest when the food availability was lowest (high food availability: $R^2 = 0.59\%$, $\beta = -0.003$, $p = .72$; medium food availability: $R^2 = 9.83\%$, $\beta = 0.012$, $p = .066$; low food availability: $R^2 = 21.10\%$, $\beta = 0.032$, $p = .002$; Figure 2). Therefore, in the variable treatment subordinate birds gained body mass in a more unpredictable way from day to day than did dominants (Figure 3).

Use of the food hopper by flocks

The coal tits in a flock spent a higher total percentage of time at the hopper in the early morning (repeated measures ANOVA within flock, with the percentage of feeding opportunities taken as the dependent variable, food availability as a

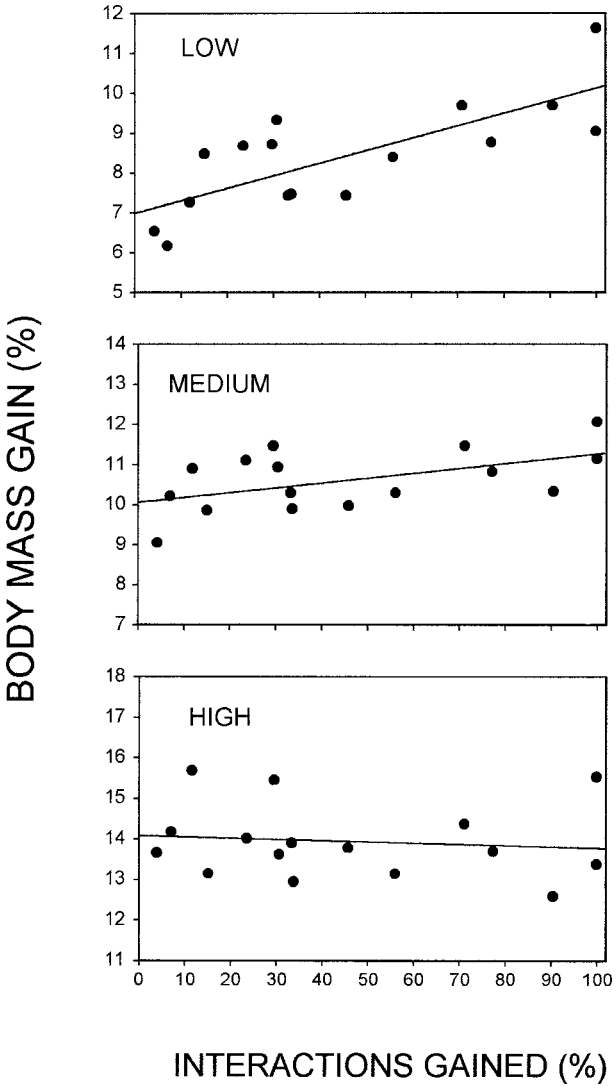

Figure 2
Mean percentage weight gain each day by coal tits in relation to their dominance status. The data are shown separately for three levels of food availability. The dominance rank of each bird is expressed as the percentage of paired aggressive interactions that it won. Differences between flocks were standardized by calculating separate regression analysis of the percentage of body mass increase for each flock. The residuals of such analyses, added to the mean value, are shown in the figure.

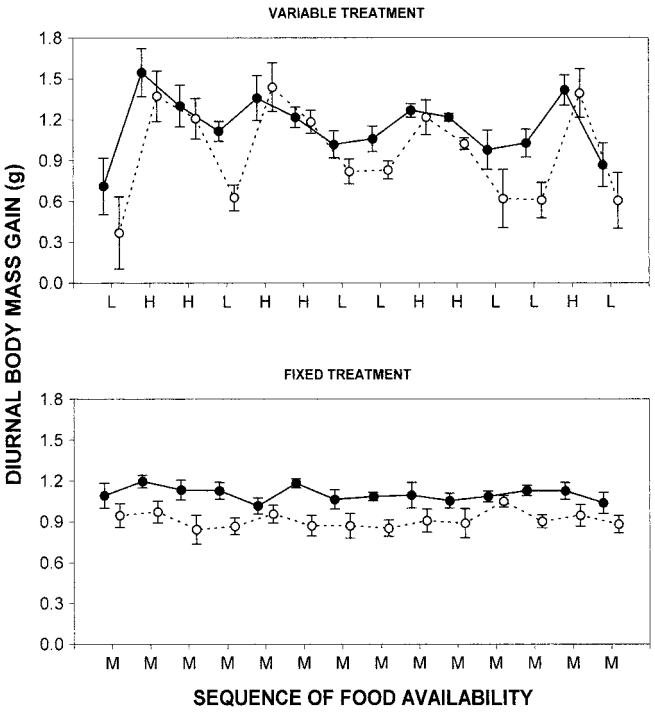

Figure 3
Mean (±SE) diurnal increase of body mass of the most subordinate bird (open circles, lighter lines) and the most dominant bird (filled circles, darker lines) of each flock in the variable treatment and in the fixed treatment. Each data point is the average of four birds in each day of the treatment sequence ($n = 4$).

fixed factor, and flock number as the blocking factor; 94.6 vs. 74.6%, comparing morning vs. evening, $F_{1,17} = 107.05$, $p < .001$). Food availability also affected the percentage of time at the hopper (93.8, 79.6, and 81.1% when food availability was low, medium, and high, respectively; planned comparison low vs. medium or high food availability: $F_{1,17} = 23.56$, $p < .001$). In addition, the differences in the intensity of feeder use between morning and evening changed comparing low with medium or high food availability (interaction between time of day and food availability: planned comparison, $F_{1,17} = 87.91$, $p < .001$; Figure 4). There were also significant differences between flocks in their relative time spent at the food hopper (blocking effect: $F_{3,17} = 6.15$, $p = .005$).

The hopper was shared with other birds on 35.4% of occasions in the morning but 12.2% in the evening (repeated measures ANOVA within flock comparing morning vs. evening, respectively, $F_{1,17} = 34.65$, $p < .001$). There were differences in this shared use of the feeder with the level of food availability (32.6, 21.1, and 17.6% in the low, medium, and high food availability, respectively; planned comparison low vs. medium or high food availability: $F_{1,17} = 21.30$, $p < .001$), and these differences changed with time of day (interaction between time of day and food availability: planned comparison, $F_{1,17} = 24.30$, $p < .001$; Figure 4). The extent of hopper sharing also varied between flocks (blocking effect: $F_{3,17} = 5.58$, $p = .008$).

The rate of aggressive encounters changed with time of day (repeated-measures ANOVA within flock; 1.15 vs. 0.54 attacks per minute, comparing morning vs. evening, respectively, $F_{1,17} = 20.98$, $p < .001$) and with the level of food availability (1.04, 0.69, and 0.80 attacks per minute in the low, medium, and high food availability, respectively; planned comparison low vs. medium or high food availability: $F_{1,17} = 4.89$, $p = .04$). The temporal pattern of aggression also varied with the level of food availability (interaction between time of day and food availability: planned comparison, $F_{1,17} = 20.27$, $p < .001$; Figure 4). There were no significant differences between flocks in the aggression rate (blocking effect: $F_{3,17} = 3.02$, $p = .06$).

In summary, the feeder was used more intensively (and was more often shared) in the early morning than in the evening, regardless of the level of food availability. As a consequence, aggression rates were also higher in the morning than in the evening and were higher when food availability was low.

Dominance rank and visits to the food hopper

To examine the effect of social rank on access to food, we used the mean percentage of time that each rank of bird spent at the hopper as the repeated factor in a repeated measures ANOVA for each flock, with food availability and time of day as fixed factors. There was a significant effect of social

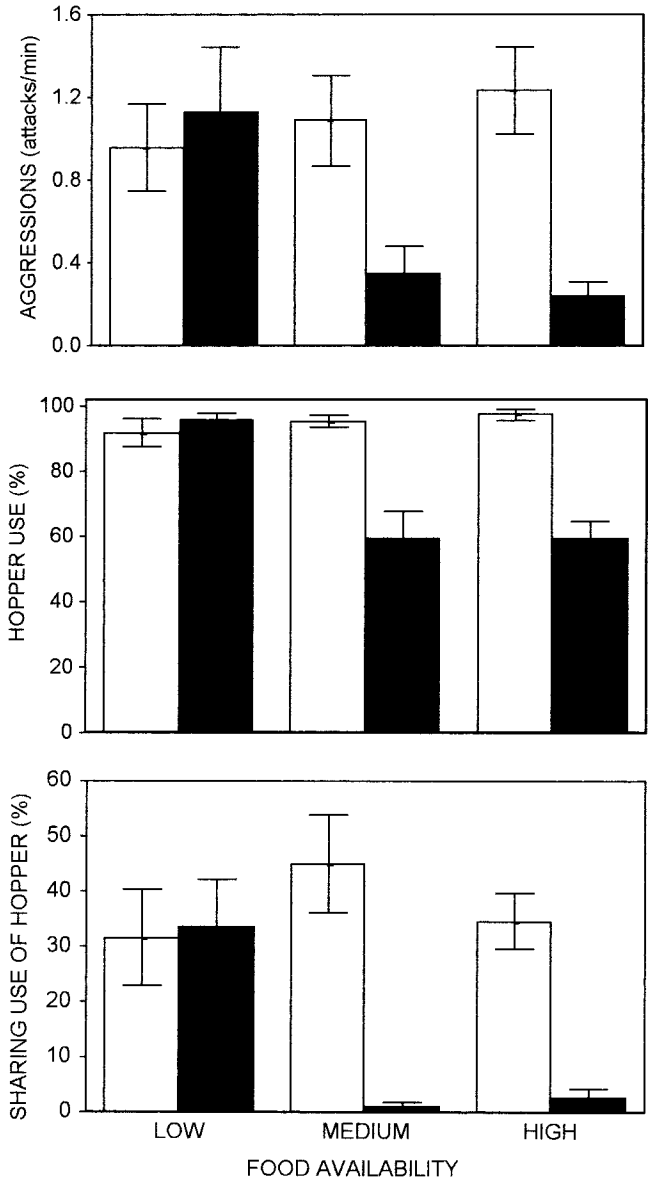

Figure 4
Mean (±SE) rate of aggressive encounters (top graph), percentage of time the hopper was occupied (middle graph), and percentage of time the food hopper was occupied by more than one bird (bottom graph) in three levels of food availability, in the early morning (open bars) and late evening (filled bars). Data are the average of four flocks and two or three observations at each time of day and food availability (n = 8–12 observations per bar).

rank on access to food (the more dominant the bird, the greater the percentage of time at the hopper; planned linear comparison by dominance rank: $\chi^2 = 60.75$, df = 8, $p < .001$; combined probability test; Figure 5). Birds visited the hopper more often in early morning than in the evening (morning vs. evening comparison: $\chi^2 = 60.05$, df = 8, $p < .001$; Figure 5), and when food availability was low compared to when it was medium or high (low vs. medium or high food availability, planned comparison: $\chi^2 = 24.69$, df = 8, $p = .002$). Nevertheless, the effect of dominance status on the percentage of time spent at the hopper was stronger in the early morning than in the evening (interaction, dominance rank × time of day: $\chi^2 = 26.39$, df = 8, $p < .001$) and when food availability was lower (interaction, dominance rank × level of food availability, with planned comparison low vs. medium or high food availability: $\chi^2 = 35.47$, df = 8, $p < .001$). In summary, subordinate birds gained least access to the food when food availability was scarce and at the beginning of the foraging period each day.

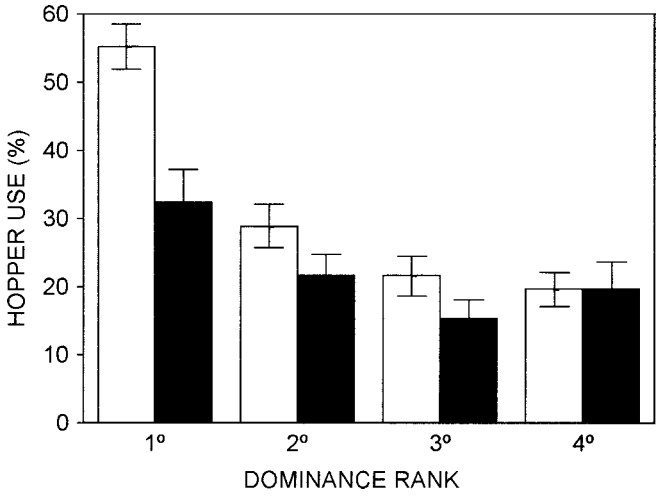

Figure 5
Mean (±SE) percentage of time the food hopper was occupied by each bird of the flock in early morning (open bars) and late evening (filled bars). Birds are arranged by their dominance rank from the most dominant (1°) to the least (4°). Data are presented as the average of four birds, with seven observations per bird (n = 28).

DISCUSSION

The coal tits in our experimental study responded to the unpredictable alternation between high and low food availability by increasing the variability in both morning and evening body mass and by increasing variability in the body mass gained during the day. Furthermore, it is noteworthy that body mass became more variable at dusk than at dawn. Both results are in agreement with predictions. As a consequence of stochastic foraging success inherent in most natural environments, on unfavorable days birds will not satisfy their full energetic demands, thus increasing the variability in body mass among days, and consequently the risk of suffering starvation. A similar argument is well illustrated in Hurly's work (1992; see Figure 1).

In natural conditions, the risk of starvation is high at the start of the day, when body reserves reach their minimum level, but also high at the end of the day, when birds go to roost ant their body reserves may be insufficient to last the night. A possible strategy to cope with the effects of highly variable food availability on body reserves is to adjust the variability of such body mass at the start of the day to minimize the immediate risk of starvation (but see Thomas, 2000). An adjustment of the variability in body mass in response to variable food supply has been also reported in other species (e.g., the marsh tit, *Parus palustris*; see Hurly, 1992). In Hurly's (1992) study, marsh tits that experienced high temporal variations in food supply maintained the variability of body mass during the day, while increasing their hoarding and recovery rates from external hoards. In our study coal tits were prevented from hoarding food overnight. Perhaps in response to this, the birds appeared to reduce the variation in body mass at the beginning of the foraging period (i.e., the time of day where the immediate risk of starvation was highest). This reduction in the variability in morning body mass was achieved

by adjusting the rate of mass loss during the previous night (i.e., the lower the evening body mass, the lower the body mass loss during the night).

Overnight mass loss in small birds may not necessarily be strategically adjusted but may be simply a consequence of mass-dependent mass loss (see Reinertsen, 1996). Small birds may regulate the degree of hypothermia according to their evening body weights (Reinertsen, 1996; Reinertsen and Haftorn, 1986). This adjustment of body mass loss has been reported in free-living individuals of all *Parus* species (see Haftorn, 1992). However, it would be difficult to accept an overnight regulation of mass lost by hypothermia in our birds because the temperature in the experimental cages was too warm. In an experimental study, Bednekoff and Krebs (1994) used both a warm overnight temperature of 15.5°C and a cold one of 1.5°C and found a similar nightly weight loss in great tits dependent upon evening body mass, but not dependent upon overnight temperature. These results suggest that other factors in addition to overnight temperature might affect overnight mass loss. Nevertheless, it should be noted that the warm temperature used in our experiment, which is very different from the cool temperature in wintering birds at high latitudes, might influence the bird's perception of starvation risk.

In a related study, Thomas (2000) used days with and without food supplementation to manipulate the body reserves of free-living European robins, *Erithacus rubecula*. Robins showed a greater variability in body mass at dawn than at dusk. Thomas (2000) suggested that when food is superabundant, birds attempt to reach a constant level of reserves at dusk, regardless of their reserves at dawn. We think the conclusions of Thomas (2000) cannot be exactly applied to our results because, first, the studies were conducted under different manipulation scenarios (food supplementation in European robins vs. food supplementation and deprivation in coal tits), and, second, the experiments were of different duration (4 days vs. a month in this study). Coal tits can easily recover from short and unpredictable periods of food deprivation (Carrascal and Polo, 1999). Therefore, the lower variability in body mass at dusk in European robins (Thomas, 2000) could also be, in our opinion, a consequence of the relative capacity of the birds to adapt to unfavorable shorts feeding periods. Third, a more important consideration is that in the study of Thomas (2000) and in the study of Lilliendahl et al. (1996), food was available ad libitum throughout the days on which body mass was monitored. In these circumstances, the birds were not constrained by food availability, access to feeders, and so on, in contrast to the coal tits in the present study. Fourth, we also do not disregard possible differences between species in their response to food manipulation. For example, robins and great tits do not cache food under natural circumstances, in contrast to coal tits. Differences between coal and great tits might have arisen from their differences in size (i.e., higher surface area-to-volume ratio and metabolic cost in coal tits than in great tits) and social rank in natural conditions (i.e., great tits being of higher rank than coal tits in mixed-species groups).

Another possible strategy to avoid starvation in response to an unpredictable food supply would be to increase mean body mass. Short-term changes in body mass in birds mainly reflect differences in fat reserves (Blem, 1990), and building up evening fat reserves normally allows small birds to survive the night and part of the next day (Blem, 1976; Jenni and Jenni-Eiermann, 1987; King and Farner, 1966). Theoretical models predict that a larger body mass would be insurance against the uncertainty of gathering enough reserves in days with low food availability (Bednekoff and Houston, 1994; Houston and McNamara, 1993; Houston et al., 1997; Lima, 1986). This prediction is supported by various laboratory and field studies that examined the effect of variability of food availability and foraging time (Bednekoff and Krebs, 1995; Ekman and Hake, 1990; Pravosudov and Grubb, 1997; Swennen et al., 1989). Surprisingly, the coal tits in our experiment did not significantly increase their mean body mass at dawn when food availability changed in unpredictably among days (see Dall and Witter, 1998; Hurly, 1992, for analogous results). Instead, the tits increased their foraging intensity and, as a consequence, the incidence of both sharing access to the feeder and aggressiveness.

When a day of high food availability was followed by a second day with high food availability, the increase in body mass was smaller on the second than on the first day. Therefore, coal tits used their first opportunity of increased food availability to recover from a previous day where food was scarce. We cannot discard the potential effects of mass-dependent predation risk on daily body mass gain because birds carried less mass on the second day with high food availability (Carrascal and Polo, 1999; Cresswell, 1998; Gosler et al., 1995).

As expected, dominant birds had priority of access to the food hopper, as found in other flocking species (e.g., Ficken et al., 1990; Senar et al., 1990). Although this had little effect on subordinate coal tits on days of medium or high food availability (i.e., there were no differences between subordinate and dominant birds in the percentage of daily mass gained), on days with low food availability the increased competition at the feeder resulted in subordinates gaining less body mass and being unable to reach the evening level of fat reserves of more dominant birds (as also found by Langen and Rabenold, 1994). As a consequence, when food availability was unpredictable between days, subordinate coal tits showed a greater variability in both daily mass gain and evening reserves than dominants (Figure 3). Therefore, the likelihood of starvation in days of food shortage could be greater in more subordinate birds (Blem, 1990; Ekman, 1990; Houston and McNamara, 1993).

In natural habitats, when food resources are limited, subordinate tits may move (or are displaced) to foraging sites where competition is reduced but predation risk is higher (Lens et al., 1994), or they may forage at times of the day when foraging conditions are worse (e.g., Lahti et al., 1997). These behavioral differences from dominant birds could reduce their survival (Hogstad, 1988; Koivula et al., 1994). When these alternatives are not available, as in our experiment, subordinate birds may be forced to adopt a lower body mass. This lower body mass need not be a strategic response, but a simple result of the different degrees of access to food available to birds of different dominance rank.

Several studies have indicated that subordinate birds may carry larger fat reserves than higher ranked birds during winter (e.g., Ekman and Lilliendahl, 1993; Gosler, 1996; Hake, 1996). Increased body reserves would allow subordinate birds to survive in periods of food shortage, when dominant birds occupy the best foraging sites (Clark and Ekman, 1995; Ekman and Lilliendahl, 1993; Gosler, 1996; Hake, 1996). However, in our experiment, subordinate coal tits did not have greater body reserves than dominants when the access to food between consecutive days was less predictable. Instead, birds with low social status increased the variability in daily body mass gain during the course of the experiment than more dominant birds. This apparent discrepancy between published experiments may be due to differences in the method used to manipulate the unpredictability of access to food (see, e.g., Cuthill et al., 2000; Kacelnik and Bateson, 1996, for confounding effects of the manipulations in mean, variance, and unpredictability of the food supply on body mass regulation) or in the behavioral ecology of the species.

Even though it has generally been assumed that an increase in fat levels is the main response to cope with an uncertain food supply, some studies have shown that there are alternative strategies (e.g., Hurly, 1992; working with marsh tits, *Parus palustris*). In species like marsh and coal tits, energy may be saved not in the form of body reserves but externally, in the form of food caches (Hurly, 1992). By relying on external caches rather than on internal reserves, hoarders can avoid some of the costs associated with an increased body mass (Houston et al., 1997; Metcalfe and Ure, 1995; Witter and Cuthill, 1993). Therefore, when new food is difficult to obtain, subordinate birds should turn to their food caches sooner than dominant birds (Vander Wall, 1990). In our experiment, coal tits were observed using short-term food stores, filling them in the morning and retrieving food from them in the evening. Indeed, we observed subordinate birds removing food from the hopper and putting it in other parts of the cage when food availability was high, as if they were building a food cache. However, we cleaned the cages and recovered all this food at the end of each day, which may be one reason why subordinate birds experienced such a drop in body mass on the next day of low food availability; they were not able to use their food cache the following dawn. Therefore, although subordinate birds were affected most by the variable treatment, it seems that they resorted to food hoarding to some extent. Thus, we might expect that those birds suffered more in the experiment that they would in the wild. Our experimental design may have prevented at least some of the birds from following the optimal mass at dusk (e.g., Thomas, 2000). The results of our study suggest that further experimental studies on the role of food caching in the strategic regulation of energy reserves are required to fully understand the social context of foraging decisions in small birds.

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