

# Social stability and daily body mass gain in great tits

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This paper presents the results of an experiment on the influence of changes in flock composition and social rank on the pattern of daily mass gain in captive wintering great tits. We created flocks of three male great tits and scored dominance when ranks had stabilized after a few days. We then moved the dominant bird from each flock into a neighboring flock, thus creating a certain amount of social instability and unpredictable resource access. Both before and after moving the dominants, we collected individual body mass data three times a day. When the hierarchies had stabilized in the second flocks, individual ranks were scored. After the dominant birds were moved, the rate of daily mass gain increased for the average individual. There was also a decrease in average morning body mass, so the birds started the day at a lower mass and ended at a slightly higher mass than previously. Dominants were on average heavier than subordinates, but we found no statistically significant effect of rank change on body mass. The pattern of daily mass gain was linear over time both before and after treatment. We conclude that an impression of unpredictable resource access can be created by disturbing the social structure in a flock, with similar effect as from restricting individual access to feeders. Within a flock, instability of the social hierarchy thus seems to have an influence on body mass management in addition to that of environmental stochasticity. *Key words:* resource access, social dominance, *Parus major*, passerines. [*Behav Ecol* 15:549–554 (2004)]

Small passerines living in temperate climates are known to adjust their body mass according to latitude, season, and the ambient temperature and weather conditions (Blem, 1975, 1976; Haftorn, 1989; Lehikoinen, 1987; Lilliendahl, 2002; Lima, 1986). In winter, the individual's body mass increases over the course of a single day, due to the acquisition of fat deposits needed to meet the energy requirements during the night (Ekman and Lilliendahl, 1993; Gosler, 1996; Lehikoinen, 1987). The daily mass increase is usually well below the physiologically possible level, which may indicate a trade-off between starvation and predation risk (e.g., Lima, 1985; McNamara and Houston, 1990; Witter and Cuthill, 1993). The daily mass gain also depends on the foraging situation: the time and energy required to forage (Witter and Cuthill, 1993) and the predictability of resource access (Bednekoff and Houston, 1994; Bednekoff and Krebs, 1995). Resource access for the individual may be influenced by environmental factors such as day length, adverse weather, and snow cover (Gosler and Carruthers, 1999; Haftorn, 1989), but also by social factors such as group composition and social status (Gosler, 1996; Gosler and Carruthers, 1999; Witter and Swaddle, 1997). The main pattern of adjustment to such factors is that the body mass gain is greater over the day, when resource access is less predictable or more variable (Bednekoff and Krebs, 1995; Gosler, 1996; McNamara et al., 1994). It has also been suggested that resource variability may cause peaks in foraging activity in the morning and in the afternoon, to hedge against starvation and at the same time avoid predation. Furthermore, when resources are scarce the rate of body mass gain can increase (Gosler, 1996), so the magnitude of daily mass gain is greater as well as accrued during a shorter time, whereas under more predictable conditions the foraging is more uniformly spread out over the day and consequently mass increase is relatively linear (Gosler, 1996). Another

factor affecting daily mass gain is hoarding activity (e.g., Ekman, 1989; Pravosudov and Grubb, 1997). When comparing the feeding habits of hoarders and non-hoarders, Lilliendahl (2002) found that hoarding willow tits (*Parus montanus*) have peaks in foraging activity and mass gain in the early part of the day, while non-hoarders (like the great tit [*Parus major*]) exhibit a more linear increase over the day, a pattern which has also been predicted by theoretical models (e.g., Brodin, 2000; McNamara et al., 1990).

Parids wintering at high latitudes often live in social groups and forage together (Ekman, 1989; Ficken et al., 1990; Saitou, 1978). The benefits of group-living outside the breeding season can be generally described as increased foraging efficiency and better protection against predation, but at the price of competition for resources. For species living in dominance-structured groups, there is often a difference between dominant and subordinate individuals in the amount of body reserves they carry (Ekman and Lilliendahl, 1993; Haftorn, 1992, 2000; Hogstad, 1987b; Verhulst and Hogstad, 1996) and sometimes also in the pattern of daily mass gain (Haftorn, 1992; Witter and Swaddle, 1995). There seems to be no general principle determining which dominance class will be the fatter (Gosler and Carruthers, 1999; Verhulst and Hogstad, 1996; Witter and Cuthill, 1993). In many studies, the dominant individuals were found to have lower energy reserves (fat deposits) than the subordinates (Cuthill et al., 1997; Ekman and Lilliendahl, 1993; Gosler, 1996; Haftorn, 2000; Krams, 1998). In other work, however, the relationship was the opposite, with dominants being fatter than subordinates (Koivula et al., 1995; Piper and Wiley, 1990; Verhulst and Hogstad, 1996). Manipulation of individual social status by removal experiments has shown that the rise in rank of a subordinate can be associated with changes in body mass (Ekman and Lilliendahl, 1993; Verhulst and Hogstad, 1996), which could be due to a metabolic cost of dominance (Creel et al., 1996; Hogstad, 1987a; but see Bryant and Newton, 1994; Senar et al., 2000) or to strategic mass change following the rank shift (Cuthill et al., 1997; Ekman and Lilliendahl, 1993; Verhulst and Hogstad, 1996; Witter and Swaddle, 1995). The combination of social rank and environmental factors may

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Received 4 March 2003; revised 14 August 2003; accepted 27 August 2003.

have a strong effect on individual resource access—and thereby on the pattern of daily mass gain. Another possible cost of changes in flock composition could be a greater amount of time allocated to aggressive interactions involving physical exertion and leaving less time in which to forage. Increased rates of social interactions could also be accompanied by increased metabolic demands, at least for high-ranking individuals (Cristol, 1995).

Great tits living in winter flocks have a relatively stable linear dominance hierarchy, with old birds usually dominating young, and males dominating females (Ekman, 1989; Hogstad, 1989; Saitou, 1979). They live opportunistically, scavenging and covering relatively wide areas when foraging (Cramp and Perrins, 1994; Glutz von Blotzheim and Bauer, 1993), and they presumably experience large natural variation in resource availability.

Since dominants and subordinates may have different fattening strategies while competing for the same food resources, the dominance hierarchy or social 'environment' can be considered an important influence on the predictability of resource access for the individual. In a stable dominance hierarchy, individuals of different ranks would be expected to follow their usual patterns of mass gain. However, if the hierarchy is changed, disrupting the social stability of the flock, we might expect changes in individual choice of mass gain strategy, because the individuals may perceive the new resource situation as more insecure compared to the previous one.

In this paper we present the results of an experiment in which we manipulated the social stability in winter flocks of great tits. The manipulation consisted in switching the dominant individuals between flocks, thus altering flock composition while keeping flock size constant. This was done not primarily to study mass gain for individuals rising in rank, but rather to see the effect of increased variability in resource access—caused by the social instability—on body mass levels of both dominants and subordinates. In addition, we wanted to see if there were any general effects on the pattern of daily mass gain. We predicted that the variation in individual body mass would increase when the social situation became unstable, because of increased interaction rate between individuals, stressful uncertainty regarding own position in the hierarchy, and uncertainty of access to food (Balph, 1979; Cristol, 1995; Polo and Bautista, 2002; Witter and Goldsmith, 1997; Witter and Swaddle, 1995). We also predicted that the rate of daily mass gain would increase, as individuals might strive to reach a sufficient level of body reserves earlier in the day (Bednekoff and Krebs, 1995; McNamara et al., 1994). Finally, we predicted that rank shifts after manipulation would result in lower body mass for individuals rising in rank and vice versa, consistent with the idea of strategic mass management (Ekman and Lilliendahl, 1993; Gosler, 1996; Witter and Swaddle, 1995).

## METHODS

### Study animals and experimental setup

The study was carried out at Tovetorp Zoological Research Station in south central Sweden between 27 November 2001 and 5 March 2002. During this time, the outdoor temperature varied from  $-25$  to  $+12$  degrees C. Nine flocks of 3 great tits were used (permit Dnr. 51-01 by the Linköping ethical board for conducting behavioral research). All the birds were male and the majority (20 out of 27) were in their first winter (age was scored according to Svensson [1994]). The birds were wild-caught in the vicinity of the research station and subsequently released in the same area. We used 4 capture sites located

between 3 and 10 km apart to avoid mixing acquainted birds in the first flock. Great tit basic flock home ranges are usually below 500 m in radius (Saitou, 1979). The site fidelity of the great tits within a basic flock in our study population lasted for several weeks (H. Lange, personal observation), supporting the notion that such flocks remain a stable unit, even though membership may gradually change over time. To trap the birds we used a small wire-net cage baited with sunflower seeds and equipped with a remote-controlled trap door. After capture they were color banded and grouped into flocks, each individual spending its entire period of captivity in the outdoor aviaries where the experiments were performed.

There were three non-roofed aviaries measuring 2.5 m (W at inner end)  $\times$  5.5 m  $\times$  4.5 m (W at outer end)  $\times$  2.2 m (H). Each contained two remote-controlled seed feeders, two remote-controlled suet-cake feeders, a variety of perches, three nest boxes in which to roost, and some branches and bushes for shelter. The nest boxes facilitated capture of the birds while still asleep, before moving or releasing them. There was also an electronic balance (Precisa 310C, IP65, external display) placed in a plastic box to protect it from the elements. The weighing cup protruded from the top of the box and was placed below the end of a blow tube from which mealworms could be dispensed.

The birds were fed commercial sunflower seeds and suet cakes, as well as homemade "trial" suet-cakes, consisting of a mixture of chopped mealworms, ground sunflower seeds, and suet molded into cakes, which seemed quite attractive to the great tits. The suet cake feeders, used for dominance trials, allowed easy access to only one bird at a time, but they had a 20-cm long array of perches attached, along which intruders could approach the feeding bird. Observations were made using video cameras (Panasonic NV-DX100 digital video) that were set up in fixed positions outside the aviaries, facing the trial feeders and balances.

### Experimental treatment and data recording

After being introduced into the aviary, birds were kept for 3–5 days on ad libitum food, including occasional access to trial food, during which time dominance ranks could establish. Verbeek et al. (1999) report that the time required to develop a stable hierarchy in a flock of 5–7 great tits ranges from 3 to 11 days, with top and bottom ranks stable already after 3–5 days. After the initial period, dominance interactions were recorded by preventing access to food and then opening a single trial feeder. This was performed twice, with one day of ad libitum food in between (for details of dominance scoring, see Lange and Leimar [2003]). After one more day, the experimental treatment was applied: in the hour before dawn; we moved the dominant bird from each aviary into a neighboring one. This was done in a randomized sequence (clockwise or counter-clockwise) so that all dominants started the next day in a new flock and a new aviary. After another two days, dominance was scored in the re-arranged flocks.

During the period from the day after capture until the hierarchy in the post-treatment flocks had been established, the birds were weighed by remote control three times daily: in the morning, at noon, and one hour before dusk. The weighings were recorded on videotape (the visiting bird and LED display) to ensure the reliability of identification. The tapes were subsequently transcribed onto Microsoft Excel spreadsheets. After the post-treatment dominance hierarchy had been assessed, the birds were released in the same area where they had been caught.

Feeding generally started at first light, continued during the morning, and grew less intense after midday. After 1500 h, there was little or no foraging activity as daylight started to

**Table 1**  
Analysis of variance of body mass

Effect	<i>F/Z</i> <sup>a</sup>	df <sub>num</sub>	df <sub>den</sub>	<i>p</i>
Dominance	4.71	1	18	.044
Rank change	0.25	2	18	.78
Treatment	5.43	1	21	.030
Time of day	427.26	1	21	<.0001
Treatment × Time of day	11.99	1	21	.002
Individual (Dominance × Rank change)	2.69 <sup>a</sup>	—	—	.004
Individual × Treatment	1.59 <sup>a</sup>	—	—	.056
Individual × Time of day	1.44 <sup>a</sup>	—	—	.076
Individual × Treatment × Time of day	0.73 <sup>a</sup>	—	—	.23
Day (Individual)	6.30 <sup>a</sup>	—	—	<.0001

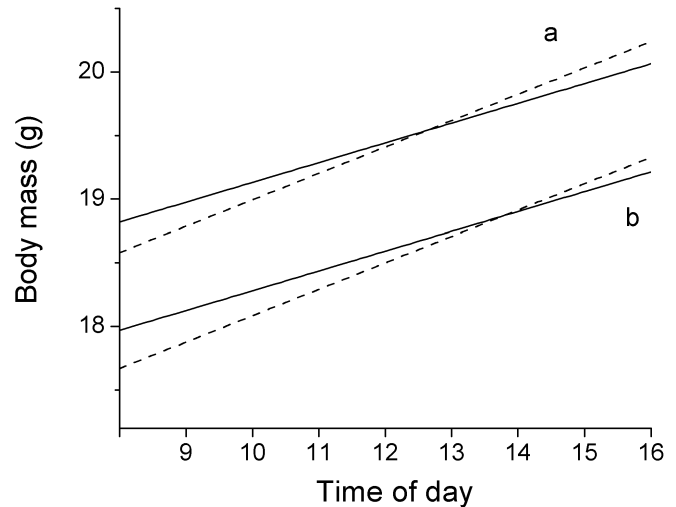
A linear mixed model was fitted to the body mass data with dominance category (dominant/subordinate in the first flock), rank change (up/down/no change), and experimental treatment (before/after) as fixed factors; individual ( $N = 22$ ) and day as random effects factors, and time of day as covariate. The intercept for time of day was 0800 h. The notation A (B) used for effects means that A is nested in B. A primary reason for including the various random effects involving individual was to properly account for the individual as sampling unit. The analysis was based on 579 weighings.

<sup>a</sup> Wald's Z-values are given for random effects.

wane (but mealworms at the balance were still attractive). Most of the great tits were easily accustomed to the daily weighing routine, although a few individuals would refuse to approach the balance. These individuals were excluded from the analysis, along with any individuals lacking sufficient mass data points (i.e., less than three points either before or after applying the treatment) to allow the fitting of a linear model. This left a total of 22 individuals out of the original 27 to be included in the linear model and 8 flocks out of 9 in the flock-level comparisons. The number of mass recordings for an individual for each treatment period varied considerably (before: range = 3–21 recordings, mean = 15; after: range = 7–17 recordings, mean = 12). In no case did moving the dominants lead to serious aggression or injury of the birds involved.

### Statistical analysis

For statistical analysis, an important aspect of the data was that several body mass recordings were obtained from an individual bird. We took the between-individual variation into account by using a linear mixed model when performing analysis of variance of the body mass data. We also took into account the day-to-day random variation in body mass by including “Day nested” in Individual as a random effects factor. For the analysis we used the mixed procedure in SAS System version 8 statistical software. We used the Akaike Information Criterion (AIC) to determine the best fitting model (Sakamoto et al., 1986). The independent variables in the linear mixed model included: Dominance (dom/sub), Rank change (up/down/no change), and Treatment (before/after) as fixed factors; Individual and Day nested within Individual as random factors; and Time of day as a covariate. We coded the sequences of ranks of an individual, which could be dom or sub before moving and dom or sub after moving, as two separate factors: Dominance before moving and Rank change. The reason for this coding was to test for effects of rank changes. To achieve a meaningful point of comparison of the body masses, we transformed the Time of day so that the intercept (time = 0)



**Figure 1**  
Linear relationship between body mass and time (fitted model). The solid lines show the rate of mass gain before moving the dominants; the dashed lines show the rate of mass gain after moving them. Lines (a) show the dominant birds and (b) the subordinate birds.

became 0800 h. This means that effects in the model not involving time of day refer to morning mass.

Although the individual bird is a natural sampling unit, there may be a danger that body mass observations from different individuals in the same flock are correlated. Thus, as a complement to the linear mixed model, we also performed flock-level analyses. To obtain flock-level data points, we averaged over the relevant flock members (i.e., the two subordinates in a flock).

### RESULTS

The best-fitting linear mixed model of body mass data is given in Table 1 and Figure 1. As could be expected, the model shows that the birds increased their body mass over the course of a day, but the rate of increase was different before and after moving the birds (Figure 1, Table 1: Treatment × Time of day). We also performed analyses including more effects than those in Table 1 (e.g., Dominance × Time of day, Rank change × Time of day, Dominance × Treatment, and a quadratic term for Time of day) but these turned out to be non-significant as well as decreasing the fit of the model as measured by AIC, so we left them out of the final fit in Table 1. This means, among other things, that we could not detect any deviation from a linear dependence of body mass on time of day.

Before moving, the average body mass increase was 1.24 g from morning until sunset, corresponding to an average rate of daily mass gain of 0.16 g per h (on an 8-h day). The average morning mass before moving was 18.3 g and the average evening mass was 19.5 g. When the dominant birds were moved, the rate of daily mass gain increased to 0.21 g/h for the average individual. There was also a decrease in average morning body mass (Table 1: Treatment), so the birds started the day at a lower mass (on average 18.0 g) and ended at a slightly higher evening mass than previously (on average 19.7 g, Figure 1). Dominants (before moving) were on average 0.8 g heavier than subordinates (Table 1: Dominance, Figure 1), but there was no significant effect of rank change on body mass. There was, however, statistically significant random variation in body mass for individuals of a given rank category (Table 1: Individual [Dominance × Rank change]) as well as statistically

**Table 2**

**Flock-level analysis ( $N = 8$ ) of the effects of dominance category and experimental treatment on residual body mass variation, obtained from the model in Table 1. The table also includes a flock-level comparison of the direction and magnitude of slope change for the two dominance categories**

Group	Residual SD $\pm$ SE	Statistic	$p$
Dominants	0.22 $\pm$ 0.02	T = 3	.04
Subordinate average	0.29 $\pm$ 0.02		
Before moving	0.23 $\pm$ 0.01	T = 8	.16
After moving	0.27 $\pm$ 0.03		

**Table 3**

	Slope change after moving		Slope change, mean $\pm$ SE
	Increase	Decrease	
Dominants	6	2	0.03 $\pm$ 0.02
Subordinates, average	8	0	0.05 $\pm$ 0.01

Dominance categories refer to ranks in the first flock. The residual SD was computed for each flock and category (averaged for subordinates) and also by splitting the residuals into before and after moving. To avoid assuming normal distributions, the Wilcoxon matched-pairs test was used throughout.

**Table 4**

	Slope, mean $\pm$ SE			$p$
	Before moving	After moving		
Dominants	0.18 $\pm$ 0.02	0.21 $\pm$ 0.01	T = 5	.07
Subordinates, average	0.15 $\pm$ 0.02	0.20 $\pm$ 0.02		
Subordinates, average	0.15 $\pm$ 0.02	0.20 $\pm$ 0.02	T = 0	.01

significant variation in an individual's body mass from day to day (Table 1: Day [Individual]). There was also a non-significant tendency for individual differences in mass change to be distinguishable after moving the dominants (Table 1: Individual  $\times$  Treatment).

We also investigated the body mass variability by analyzing the residuals from the fitted model in Table 1. Computing the standard deviation of the residuals separately for each individual and analyzing at the flock level, we found that the body mass of (first flock) dominants was less variable than that of subordinates (Table 2). To see if the experimental treatment affected body mass variability, we also computed the standard deviation of the residuals for each individual before and after moving the dominants. We could not find a statistically significant effect at the flock level, although our estimate of variability was greater after moving (Table 3). To further investigate this, the standard deviations before and after moving were also compared for each dominance class separately, but we found no statistically significant differences.

The variance heterogeneity between dominance categories (Table 2) was probably too small to affect the validity of the model in Table 1 (a conventional examination of the residuals as a function of fitted values did not suggest deviations from homogeneity). Nevertheless, we fitted a model like the one in Table 1 to data for dominants and subordinates separately. These analyses indicated a statistically significant increase for the subordinates, but not for the dominants. Furthermore, a flock-level analysis also showed a statistically significant increase for the subordinates, but only a non-significant tendency for the dominants (Table 4). Thus, we may conclude

that the subordinates increased their rate of body mass gain after the dominants had been moved, but our data do not really resolve whether the dominants reacted in the same way. Examining the slopes before and after moving for each individual separately, we found that 18 of the 22 individuals had a greater slope after moving (12 of 14 subordinates and 6 of 8 dominants).

We found no difference between body mass at capture and the body mass predicted by the model in Table 1 for the same time of day, indicating little or no general effect of captivity (body mass at capture 19.1 g  $\pm$  0.19, predicted 18.9 g  $\pm$  0.19; paired  $t$ -test:  $N = 22$ ,  $t = 1.696$ ,  $p = .105$ ). Finally, there was a non-significant tendency for the individual body mass at capture to correlate with subsequent dominance rank, although body size measured as wing length had no effect on subsequent dominance (Table 5).

## DISCUSSION

In our experiment we found that the great tits gained body mass in a linear fashion over the day and that dominants were heavier than subordinates. The magnitude of the daily mass increase in this study was 7–10% of morning mass, which is similar to other great tit studies (Haftorn, 1992; Lehikoinen, 1987).

Our experiment showed that when dominant birds were moved between aviaries, individuals (at least subordinates) increased their rate of daily mass gain (Figure 1) while at the same time their average morning body mass dropped. This suggests that the birds interpreted the change of flock composition as an unpredictable situation, regarding both resource availability and dominance positions. The uncertainty of rank, and increased resource competition along with more frequent aggressive encounters, could cause the individuals to increase their rate of mass gain to hedge against possible exclusion from resource access. Such a relation between increased rate of mass gain and unpredictable feeding conditions has also been found in other studies (Bednekoff and Krebs, 1995; Cuthill et al., 2000).

The change in morning mass differs from what one might expect from other work (e.g., Bednekoff and Krebs, 1995; Cuthill et al., 2000; Polo and Bautista, 2002), where dawn mass usually increased or remained stable under unpredictable conditions. Our results are, however, paralleled in a study by Gosler (1996), who presented data showing an increase in rate of mass gain under unpredictable circumstances and (according to his figures) a drop in morning mass.

In normal Nordic winter conditions, nightly mass loss in male great tits is roughly 7% of their evening mass (Lehikoinen, 1987). The birds in our study lost about 6.4% per night before treatment and 8.5% after, which suggests that nightly energy expenditure had increased after treatment. Previous studies (Hogstad, 1987a; Røskoft et al., 1986) have shown that the metabolic cost of being dominant was present only during daylight hours. Similar results have been found for the cost of being subordinate (Senar et al., 2000), which

**Table 5**

**Wing length, body mass at capture (mean  $\pm$  SE), and predicted body mass at capture (from the model, mean  $\pm$  SE) for dominants ( $N = 8$ ) and subordinates ( $N = 14$ ) as scored in the first flock**

Factor	Dominants	Subordinates	$t$	$p$
Wing length	77.9 $\pm$ 0.55	77.2 $\pm$ 0.52	0.88	.4
Mass at capture	19.5 $\pm$ 0.29	18.8 $\pm$ 0.23	1.91	.08
Predicted mass at capture	19.4 $\pm$ 0.35	18.6 $\pm$ 0.21		

means that cost-of-dominance effects perhaps only account for the increase in daily mass gain. A possible explanation for the nightly mass loss is that the birds went into partial hypothermia at night in the first flock (Reinertsen and Haftorn, 1986) but failed to do so in the second flock, perhaps due to elevated levels of stress hormones. It is also conceivable that the change in social situation could lead to psychosocial stress, a condition shown to be related to social defeat and which may affect body temperature, heart rate, activity levels, etc. (Carere et al., 2001), which could explain the increased nightly mass loss in terms of conflict-related increases in individual metabolic rate.

We predicted that disturbing the social situation in the flocks would lead to greater individual variation in body mass. From our observations (Table 2, 3, and 4), we cannot determine whether or not the treatment had this effect. We did, however, find that the residual body mass variance was greater for (first flock) subordinates than for dominants, which agrees with the results of Polo and Bautista (2002). The greater variability in subordinate body mass suggests that subordinates could be more strongly affected by social instability than dominants. From our data we have clear evidence that subordinates increased their rate of daily mass gain following the social perturbation, but we were unable to resolve the issue for the dominants, although the trend was in the same direction. In contrast, Cristol (1995) reports decreased rank and increased metabolic rate of dominant dark-eyed juncos (*Junco hyemalis*) that were transposed between flocks. Metabolic rate later decreased as social stability returned. The discrepancy between that pattern of reaction and the one found in members of the genus *Parus* can, as suggested by the author, probably be ascribed to differences between Paridae and Emberizidae in flock size, social system, and the longevity of flocks.

Previous studies show that under increased predation risk, subordinate great tits may have greater motivational variation than dominants in terms of aggressive behavior (Lange and Leimar, 2001). Such differences might reflect an intrinsic personality difference between dominance categories, with the subordinate personality being more sensitive to changes in the environment and also, perhaps, quicker to react to them (Verbeek et al., 1994). However, these observations might also reflect an adaptation to the unpredictable conditions of life that subordinates normally experience or, possibly, an interaction between intrinsic personality factors and a variable environment.

We also predicted that individuals changing ranks after the moving of dominants would alter their patterns of mass regulation. There were, however, few rank shifts after treatment (only 3 out of 8 moved birds changed their status), making it difficult to draw conclusions about effects of rank change on individual mass gain. From our data we can neither substantiate nor rule out that such changes in pattern of body mass gain occurred. The low incidence of rank changes does indicate, however, that any prior residence effect favoring a rise in rank of resident subordinates was quite weak compared to other dominance-determining factors. The greater changes in subordinate body mass gain after the treatment also contradict a prior residence advantage on their part. Such an effect might be expected, judging from earlier work by Balph (1979), who, in spite of her quite small sample size, reports a clear resident dominance advantage when individuals were moved between flocks of dark-eyed juncos. Again, the dissimilarities may be the result of to different social structure and group size in the two species.

Our experimental setup involved moving only the dominant birds, so the dominance categories were treated unequally, which may be regarded as a weakness. Conceivably, the

dominants experienced greater social instability, facing both new flock members and a new aviary. All else being equal, the effect might then have been a stronger reaction in the dominants. We did not observe such an effect, which is consistent with the idea of greater sensitivity in subordinates.

To conclude, we found that body mass at dawn dropped and that the rate of daily mass increase rose under induced socially unstable conditions. The effect remained statistically significant when analyzing only subordinates, but not when analyzing only dominants. This could simply reflect the low sample size, but it could also mean that subordinates are more sensitive in their reaction to social perturbations than are the dominants. In general, disturbing the social situation in dominance-structured flocks may impose similar conditions of resource unpredictability as a traditional feeder experiment would. This effect has not been studied previously, but it could well play a role under natural conditions, where social instability is likely to be present to varying degrees.

We thank Ulrika Kaby and Johan Lind for help with bird catching and Lena Näslund and Eva Åberg for animal care. We also wish to thank Juan Carlos Senar for valuable comments on the manuscript. This study was supported by grants from the Swedish Research Council (to O.L.).

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