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The effect of social dominance on fattening and food-caching behaviour in Carolina chickadees, *Poecile carolinensis*

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Subordinates often have to wait for dominants to obtain food. As a result, their foraging success should be less predictable and they should therefore maintain a higher level of energy reserves compared with dominants. A corollary of this prediction is that subordinates should gain mass earlier in the day and maintain higher mass than dominants. We tested these predictions with captive Carolina chickadees. In two different experiments (one where birds were given ad libitum access to food and the other with food access limited to 60 min/day), we formed social flocks of two previously unfamiliar birds and compared their energy management (body fat and food caches) while they were in the flock with energy management when housed alone. Results from both experiments failed to support the predictions. Of all the parameters of body mass and food caching we measured only the following results were significant: (1) On the ad libitum food schedule, both subordinates and dominants accumulated more mass over the day when in a flock compared with when they were solitary, and there were no differences in mass gain between dominants and subordinates. (2) When analysed separately, dominants showed a higher evening mass in the flock compared with the solitary condition, a trend that runs opposite to the prediction. Our results suggest that when in favourable foraging conditions, social interactions might cause dominant and subordinate birds to accumulate more energy reserves as a result of competition. On the other hand, if food supply is limited, both dominants and subordinates may be forced to maintain similar fat reserves as an insurance against increased risk of starvation.

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For permanent resident birds wintering in an environment characterized by unpredictable food, low ambient temperature and long nights, accumulating and maintaining a sufficient amount of energy is of paramount importance. However, if energy is stored as fat, the acquisition and maintenance of high fat reserves carry a number of costs. One of the primary costs associated with elevated fat reserves is the risk of predation (Lima 1986; McNamara & Houston 1990). First, an increase in fat requires more foraging, which generally can be done only by sacrificing vigilance for predators (e.g. Lima & Dill 1990). Second, birds with higher levels of fat reserves could be at higher risk of being killed by a predator if heavier birds are less manoeuvrable in flight (Witter & Cuthill 1993; but see Kullberg 1998). Thus, it has been hypothesized that birds' fat reserves are regulated as a trade-off between risk of predation and risk of starvation; as a result, birds should carry fat loads below the physiological maximum capacity (Lima 1986; McNamara & Houston 1990). This means that under otherwise constant conditions birds should compensate for an increase in starvation risk by increasing energy reserves. A number of studies have supported this view. For example, birds increase their energy reserves in response to increased risk of starvation caused by unpredictability in food supply, air temperature and unpredictable constraints on foraging time (Ekman & Hake 1990; Bednekoff et al. 1994; Bednekoff & Krebs 1995; Pravosudov & Grubb 1997).

Theoretically, daily patterns of mass gain should also reflect a trade-off between predation risk and risk of starvation. For example, McNamara et al. (1994) show that foraging activity (and a concomitant mass gain) should occur earlier in the morning as food availability or variance in access to food increases. Thus when starvation risk increases, energy acquisition should occur earlier in the day to offset this risk.

Some bird species, in addition to storing energy internally as body fat, can store energy externally as food caches. In these species, increased risk of starvation results in higher levels of cache reserves in addition to higher levels of fat reserves (Lucas & Walter 1991;

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Pravosudov & Grubb 1997; but see Hurly 1992 for results showing increased cache size but no change in body mass in response to increased variance in food supply).

The regulation of energy reserves may also be affected by social conditions. During the nonbreeding season, many resident bird species form groups with a linear social hierarchy (e.g. Piper 1997). In such groups, socially dominant individuals have priority of access to food and tend to forage in safer habitats (e.g. Ekman & Lilliendahl 1993; Lahti et al. 1998). The differential access to food and safe habitats afforded by dominance status should affect energy management tactics of both dominant and subordinate individuals. However, the effects of dominance status on energy management are difficult to evaluate because results from previous studies are contradictory. Some studies showed that dominants carry smaller fat reserves than subordinates (e.g. Ekman & Lilliendahl 1993; Witter & Swaddle 1995; Gosler 1996; Hake 1996), but other studies demonstrated that dominants maintain larger fat reserves than subordinates (e.g. Piper & Wiley 1990; Koivula et al. 1995; Verhulst & Hogstad 1996). Verhulst & Hogstad (1996) addressed this issue and proposed that the relative importance of predation risk and starvation risk in different situations could result in dominants carrying either larger or smaller fat reserves than subordinates. A dynamic model by Clark & Ekman (1995) showed that there are scenarios when dominants and subordinates should maintain similar energy reserves. Witter & Swaddle (1995) argued that there could be a continuum of possible relationships between social dominance and fat reserves. However, experimental designs might have generated hard-to-interpret results in some of these studies. For example, Ekman & Lilliendahl (1993) showed that when dominants were removed from the experimental groups, the subordinates reduced their mass. However, control groups were not manipulated, and, therefore, it is possible that removal of any birds would have the same effect through reduced competition (Witter & Swaddle 1995).

It is interesting to note that all of the experiments mentioned above used groups of more than two birds. No study to date has looked at a simple effect of dominance on energy reserves in a group consisting of just two individuals, dominant and subordinate, even though such groups are common in many resident passerines (e.g. Pravosudov 1987), including Carolina chickadees (e.g. Berner & Grubb 1985). There have been no manipulative experiments showing the effect of social dominance on food caching. Some observational data also show contradictory results with either dominants or subordinates caching more food (Pravosudov 1985; Lahti & Rytkonen 1996; Lahti et al. 1998).

Despite the contradictory results, the prediction that subordinates should maintain higher levels of energy reserves than dominants when in a social group seems to be most common in the literature (Ekman & Lilliendahl 1993; Witter & Cuthill 1993; Clark & Ekman 1995; Gosler 1996; Hake 1996). The prevalence of this prediction could perhaps be explained by the presence of a very reasonable mechanism: dominants have more predictable foraging success compared with subordinates, hence subordinates need more energy reserves as an insurance against less predictable foraging success while in the company of dominant group mates. An extension of this prediction is that subordinates should gain mass earlier in the day than dominants (McNamara et al. 1994). Here we present results of an experiment which examined the effect of social dominance on fattening and food caching decisions in social groups of Carolina chickadees consisting of just two individuals. The experiments were designed to test the prevailing prediction that subordinates, while in the presence of a dominant individual, should increase their energy reserves and they should shift the timing of their daily mass gains to earlier in the day.

METHODS

We used 28 Carolina chickadees captured at Purdue University's Ross Biological Reserve and Martel Forest near West Lafayette, Indiana. The birds were tested in indoor aviaries. The aviaries for solitary conditions were 3.0 × 3.0 × 2.1 m. A wall separating two contiguous aviaries was removed when the birds were tested as flocks, making a 3.0 × 6.0 × 2.1 m aviary.

The sexes tend to be monomorphic in chickadees, although size differences (particularly retrix and wing length) can be used to help distinguish sexes (e.g. Desrochers 1990). Size distributions of male and female Carolina chickadees in the vicinity of our capture site are published in Thirakhupt (1985). Based on this information, we tested only mixed-sex pairs (males >63 mm wing chord and females <60 mm wing chord). We always paired birds caught in different social groups to avoid testing existing pairs. Thus, we formed flocks consisting of two previously unfamiliar males and females, which had to form a social relationship under the experimental conditions. By using unfamiliar males and females in our experiments, we tried to avoid any variance in previous social relationships between experimental flock members that would confound our measure of the effect of social dominance on energy management. Although natural flocks of two birds usually contain mated pairs (Smith 1991), the members of these pairs had to form a social dominance relationship before they became mates and that is what we tried to simulate in our experiments. Each pair was caught about 2 weeks prior to testing and released after the experiment.

We started our experiments in October 1997 and the last set of birds was finished in the beginning of May 1998. For the first week, all birds were placed singly in 1-m^3 cages to habituate them to captivity, and then they were transferred into aviaries in which they were housed singly for about 3 days. A single indoor aviary contained six polyvinyl chloride 'trees', with 10 evenly spaced cache sites (each 3.5 × 7.0 × 8.0 mm) in each tree and a perch under each cache site. An infrared sensor in each cache site was used to detect the time of caching and retrieval; these data were automatically stored in a computer. Only one seed could be cached in each cache site (Lucas & Zielinski 1998). Each aviary contained one computer-controlled feeder that delivered hulled sunflower seeds and two electronic balances, one mounted under the feeder and the other one in the middle of the aviary with a perch mounted on it. A computer recorded body mass and time of day every time a bird perched on either of the two balances. When birds were solitary, their body masses were determined from the records from the separate aviaries. When birds were in a flock, one bird was always heavier than the other which allowed us to separate the records for each bird. Air temperature was constant (+19°C) throughout both experiments and photoperiod was set for an 8:16 h light:dark cycle.

We ran two different experiments, each with a treatment consisting of two levels of social interactions (flock versus solitary). All birds were tested under both treatment levels, but any given bird was tested in only one experiment. One experiment was carried out under an ad libitum food schedule while the other experiment presented a limited food schedule. Six pairs of birds were tested in the experiment with the ad libitum food schedule and eight different pairs were tested in the experiment with the limited food schedule. Two pairs were always started simultaneously; both pairs were given the same food schedule. We flipped a coin to determine which pair would start as a flock; the other birds started as two solitary birds. Each treatment continued for 10 days. After 10 days, we separated the birds in a pair by putting up a wall in the middle of the aviary (making them 'solitary') and removed the wall from the second set of aviaries letting the birds in them interact freely (flock treatment). Thus, by simultaneously testing two pairs of birds, one 'solitary-to-flock' and the other 'flock-to-solitary', we controlled for potentially confounding order effects.

During the ad libitum food schedule, the feeder delivered a single sunflower seed almost immediately after the previous seed had been taken. During the limited food schedule experiment, birds were given a total of 60 min of access to food per day spaced into four 15-min intervals during which food was available ad libitum, delivered by the computer-controlled feeder, one seed at a time. The distribution of the 15-min intervals was random except for two conditions. First, no two access intervals could be contiguous. Second, we programmed the computer to include at least one time interval during the first hour and one interval during the last hour of the day. Thus, all birds had food within an hour of the recording of evening body mass. All birds were trained on each schedule for 3–4 days before the experiment began.

At the end of each day, all birds were transferred into holding cages for about an hour so that the aviaries could be cleaned and feeders restocked with sunflower seeds. These cages were connected to the aviaries by sliding doors. Birds were induced to enter and leave holding cages by turning the room lights off and drawing them into a light source, thus eliminating the need for potentially stressful handling. In addition to the food provided by the feeders, each bird received one mealworm before night roost. Water with vitamins was provided at all times. Water for bathing was also available at all times.

During the ad libitum food schedule experiment, we observed birds' caching rate during the first 30 min of the day only. Information from the infrared sensors in each cache site was used to evaluate whether birds cached at any other time. During the limited food schedule experiment, we observed birds during the first and the last of the four 15-min time intervals when food was available. During our observations, we recorded the number of seeds taken, eaten, cached, or retrieved by each bird. We added the data from the two observation periods together to generate an index of foraging behaviour for any particular day. The conclusions were not altered if the two observation periods were analysed separately. We also used these behavioural observations to record dominance status. We recorded the number of times a bird chased its flockmate from the feeder or caused the withdrawal of its flockmate upon approach (e.g. Lahti et al. 1998); both actions were assumed to indicate dominance.

Statistical Procedures

For all statistical analyses we omitted the first 3 days of each treatment. To test the predictions we employed the following dependent variables: (1) morning body mass (recorded at 0800 hours), (2) evening body mass (recorded at 1600 hours), (3) mean daily mass gain, (4) food caching rate (seeds/15 min), (5) cache retrieval rate (seeds/15 min) and (6) food consumption rate (seeds/15 min). We used repeated measures analysis of covariance (ANCOVA) with a first-order autoregressive covariance structure (PROC MIXED; SAS Institute 1994) to analyse each experiment (ad libitum food and limited food schedules) separately. Normality of the residuals was tested using PROC UNIVARIATE (SAS Institute 1990). Consumption rates, retrieval rates and caching rates had to be $\log(x+1)$ transformed to normalize the residuals. The residuals of all other dependent variables were normally distributed.

We used treatment (flock versus solitary) and dominance status (dominant versus subordinate) as factors and number of days in the experiment as a covariate. Because birds in captivity tend to gain mass with time (Lucas & Zielinski 1998), it is important to control for the number of days in the experiment. We used a treatment × dominance status interaction to test for any differences between dominant and subordinate birds in their response to the treatment (flock versus solitary). The interaction between number of days in the experiment and treatment was nonsignificant ($P>0.10$) and was dropped from all analyses. To test statistically for any potential differences in daily mass curves between two treatments but within the same dominance status, we tested the interaction between treatment (solitary versus flock) and time of day (taken at 30-min intervals) using repeated measures ANCOVA, in which both treatment and time of day were treated as class variables (PROC MIXED; SAS Institute 1994). To test statistically for any differences in daily mass curves between dominants and subordinates within each treatment, we tested the interaction between time of day (taken at 30-min intervals) and dominance status (solitary versus flock) in the

Table 1. The effect of the treatment (flock versus solitary), dominance status and number of days in the experiment on mass in Carolina chickadees during the experiment with ad libitum food schedule

	Treatment			Dominance status			Treatment× dominance status			Days in experiment	
Parameter	$F_{1,10}$	P	Power	$F_{1,10}$	P	Power	$F_{1,10}$	P	Power	$F_{1,11}$	P
Morning mass	2.54	0.14	>0.71	21.8	<0.001		0.01	0.95	0.38	19.0	0.001
Evening mass	0.02	0.89	>0.71	27.8	<0.001		0.05	0.82	0.24	12.2	0.005
Daily mass gain	11.3	0.007		0.10	0.76	>0.71	0.32	0.58	>0.71	8.6	0.014

repeated measures ANOVA, in which both time of day and dominance status were treated as class variables. If daily mass curves differed between the treatments or between dominants and subordinates, a significant interaction between dominance-status and time-of-day would result.

We performed a power analysis for dominance effects and dominance interactions that were nonsignificant. The power of a statistical test represents the probability that the test will reject a false null hypothesis under a specified alternative hypothesis (Cohen 1988). Power should be calculated whenever conclusions are drawn from negative data. This is because a nonsignificant result could arise from a truly correct null hypothesis, or it could arise because the data are insufficient to detect a false null hypothesis (this latter problem is called type II error). Power can be calculated as $1-\beta$, where β is the probability of a type II error; thus high power of a test means low probability of failing to reject the null hypothesis when it is, in fact, false. The higher the power, the more meaningful are the results. The highest possible power is 1 and power higher than 0.8 is considered to be sufficient (Cohen 1988). Following Cohen (1988), we calculated an effect size for main effects and interaction effects that we assumed to be biologically relevant. For example, for the evening-mass treatment × dominance interaction, we assumed that a 0.5-g difference in the response to social effects was a reasonable alternative hypothesis to the null hypothesis of no difference. Thus, we asked what power we have to distinguish a result where the effect of treatment (flock versus solitary) on the dominant bird differed from the effect on the subordinate bird by 0.5 g (note: all tests are two-tailed). We converted this interaction strength to a standardized effect size (f; see Cohen 1988, page 371) using an estimate of the variance of the data cells in the denominator (within-cell population standard deviation) of the relevant F test. Our variance estimates were generated using restricted maximum likelihood (REML) estimates generated by PROC MIXED.

We tested two different types of dependent variables related to mass: absolute mass (morning mass or evening mass) and change in mass (mass gain from morning to evening). For tests with absolute mass as a dependent variable, we assumed that a response of at least 0.5 g was a reasonable alternative hypothesis to the null hypothesis of no change. The effect strength is based on our previous studies of mass regulation in this species (e.g. Lucas & Walter 1991; Lucas 1994; Lucas & Zielinski 1998). We used this 0.5-g effect to calculate power for both main effects and for interactions (i.e. as outlined in the example). We used the following logic for tests relating to changes in mass. The average change in mass from morning to evening was about 0.8 g. We assumed that a significant response to our treatment would result in a change in mass gain of about 10% or more of this average (i.e. 0.08 g). We used the 0.08-g value to calculate power for both main and interaction effects. Similarly, we used this 10% rule to generate effect sizes for consumption rates (mean log(consumption+1)=2.2, so effect size was 0.22) and caching rates (mean log(cache rate+1)=1.1, so effect size was 0.11). Finally, note that the power to detect a 0.5-g main effect can be over twice the power of detecting a 0.5-g interaction effect (see Cohen 1988).

RESULTS

Larger birds always dominated smaller birds with no exceptions ($N>10$ of interactions for each pair; binomial test: $P<0.01$). Thus, we assume that dominance status was rapidly attained and was maintained over the course of the experiment.

Ad Libitum Food Schedule

Both dominants and subordinates gained significantly more mass during the day when in a flock than when solitary (Table 1, Fig. 1c). However, neither morning mass nor evening mass alone showed a significant difference between flock and solitary treatments in either dominants or subordinates (Table 1, Fig. 1a, b). There were also no differences in either body mass parameters between dominants and subordinates as reflected by the treatment × dominance status interaction (Table 1). The power of the interaction effect was low (<0.40, Table 1). However, extremely low F values (<0.05; Table 1) and nearly identical increases in mass in response to the treatment (i.e. flock versus solitary environment; Fig. 1) both suggest that the lack of interaction is real.

There was a significant effect of dominance status on both evening and morning body mass (Table 1). This simply confirms the fact that dominant birds were always heavier than subordinates; indeed, the difference between pair members was dictated by the experimental design. In addition, both dominant and subordinate chickadees increased their morning and evening mass throughout the experiment ('Days in experiment' effect in Table 1).

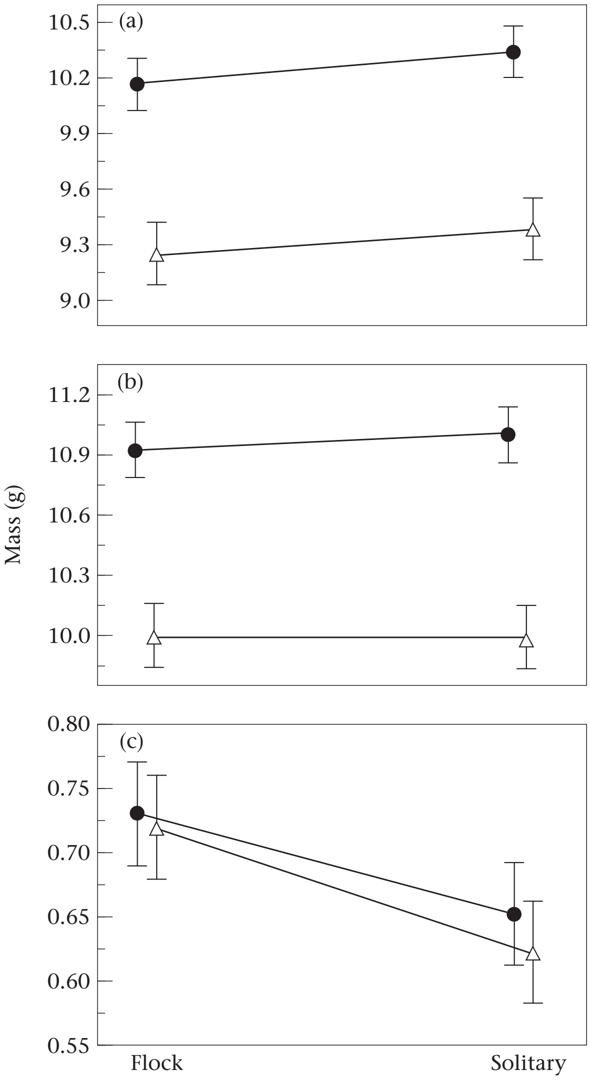

Figure 1. Effect of social dominance on energy reserves in Carolina chickadees during the experiment with ad libitum food schedule. Presented are least squares means with standard errors (calculated by PROC MIXED: SAS Institute 1994) of dominants (●) and subordinates (△) when in a flock and when solitary. (a) Morning body mass; (b) evening body mass; (c) mean daily mass gain.

Neither subordinates nor dominants changed their daily patterns of mass gain when housed as a flock compared with when they were solitary (repeated measures ANOVA: time of day-treatment interaction, subordinates: $F_{16,165}$=0.05, P=0.99; dominants: $F_{16,165}$=0.15, P=0.99; Fig. 2). The power to detect a 0.5-g interaction effect was greater than 0.95 for both comparisons. In addition, we compared dominant to subordinate mass trajectories by standardizing each curve to deviations about a daily mean of zero (thus statistically cancelling out the effect of the difference in absolute mass between dominants and subordinates on mass trajectories; see Hurly 1992). The daily mass trajectories of subordinate and dominant birds were nearly identical during both solitary and flock treatments indicating that dominance status had no effect on the way the birds accumulated their energy reserves during the day (repeated measures ANOVA: time of day dominance status interaction, solitary: $F_{16,160}$=0.47, P=0.96; flock: $F_{16,160}$=0.67, P=0.82; Fig. 3). The power to detect an interaction effect of 0.25 g (e.g. the subordinate gains 0.25 g more than the dominant over the day) exceeded 0.95 for both treatments.

Dominant birds never cached food in the experiment with the ad libitum food schedule during the focal samples. Of six subordinates, only two individuals cached food and these birds cached more when in a flock than when solitary (subordinate 1: 4.67 ± 1.15 and 0.67 ± 0.51 caches per 30 min, respectively, in a flock and when solitary; subordinate 2: 1.23 ± 0.8 and 0 caches per 30 min, respectively, in a flock and when solitary). No statistical inference across birds could be made with this sample size in the ad libitum food experiment.

Limited Food Schedule

All measurements of body mass of dominant and subordinate chickadees showed no significant differences between solitary and flock treatments (Table 2, Fig. 4); the power of these tests was reasonably high (Table 2). There were also no significant differences between dominant and subordinate birds as determined by the treatment × dominance status interaction (Table 2), although the power of the test for evening mass was particularly low (0.30). If dominants were analysed independently of subordinates, their evening mass was higher in the flock treatment than in the solitary treatment (repeated measures ANCOVA: $F_{1,7}$=5.92, P=0.04). The same response analysed independently for subordinates showed no statistically significant differences between solitary and flock treatments ($F_{1,7}$=0.19, P=0.67).

There was a significant effect of dominance on evening and morning body mass (Table 2); this simply reflects pre-existing differences in size between dominants and subordinates. All chickadees also increased their morning and evening mass throughout the experiment (‘Number of days’ effect in Table 2).

Neither dominants nor subordinates changed their daily pattern of mass gain when they were housed as a flock compared to when they were solitary (repeated measures ANOVA: treatment-time of day interaction, dominants: $F_{16,231}$=0.3, P=0.99; subordinates: $F_{16,231}$=0.32, P=0.99; Fig. 2). The power for the test for dominants was greater than 0.95. We could not calculate an estimate of power for subordinates because the SAS routine failed to converge on an estimate of the within-cell population standard deviation. Analysis of standardized daily mass patterns of dominants and subordinates housed singly and as a flock also revealed no differences between them, and the mass curves were nearly identical (repeated measures ANOVA: time of day × dominance status interaction, solitary: $F_{16,224}$=0.64, P=0.85; flock: $F_{16,224}$=1.2, P=0.28; Fig. 3). The power to detect an interaction effect of 0.25 g (e.g. subordinate gains 0.25 g more than dominant over the day) exceeded 0.95 for both treatments.

All birds cached food in the experiment with the limited food schedule (Fig. 5). Social interactions had no

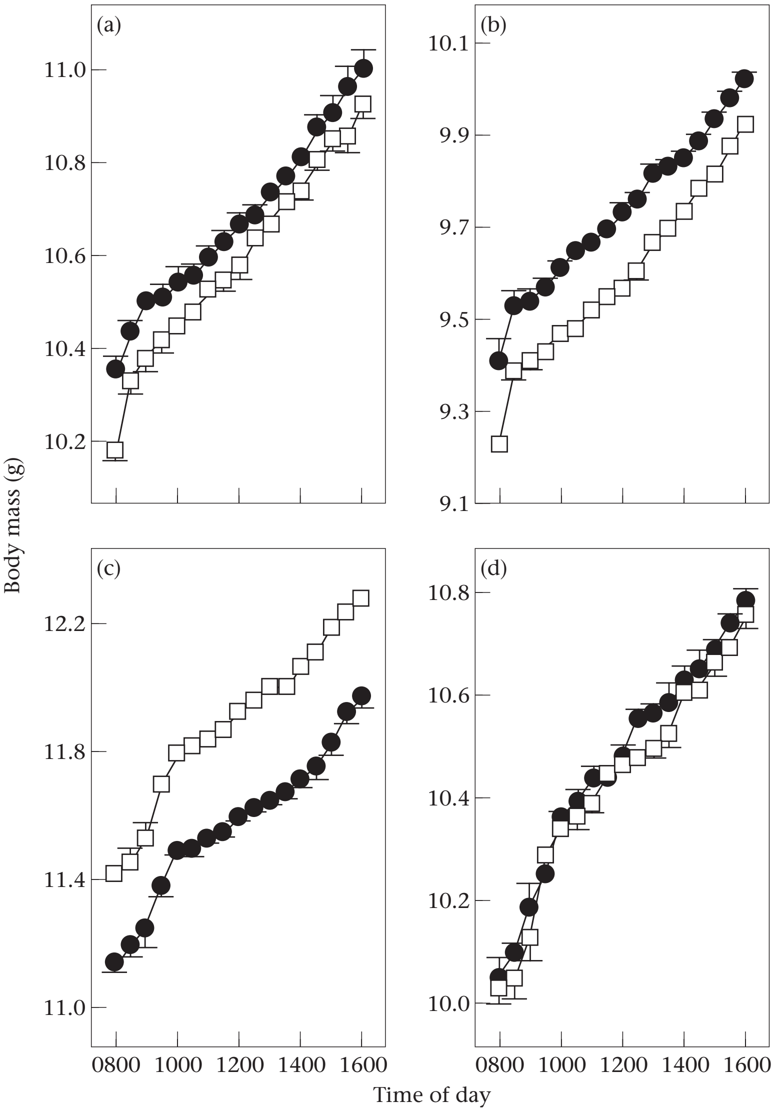

Figure 2. Daily mass patterns of dominants and subordinates on the ad libitum food schedule (a and b, respectively) and on the limited food schedule (C and d, respectively) when in a flock (☐) and solitary (●). Data represent the mean value for all birds in each category. Vertical lines represent standard error of the residual mass trajectories standardized to deviations about a daily mean of zero for overall differences in size between birds.

statistically significant effect on food caching, food retrieval and eating rates of either dominant or subordinate chickadees (Table 2, Figs 5, 6, 7). However, the power of the tests for caching rates was low and power could not be estimated for retrieval rates (Table 2).

DISCUSSION

In general, our experiments failed to support the predicted relationships between social dominance and energy reserves under either ad libitum or limited food schedules. Indeed, some patterns were opposite to those predicted. In the ad libitum food schedule experiment, we detected a larger daily mass gain in both dominants and subordinates while housed as a flock compared with mass gain under solitary conditions, and there were no differences between dominants and subordinates in this response. In the limited food schedule experiment, there were no differences between dominants and subordinates in the way they responded to the treatment, although the power of this statistical test was low. When we analysed dominant and subordinate birds separately, dominants were heavier in the evening under the flock treatment than under the solitary treatment, a result opposite to the prediction.

Both dominants and subordinates significantly increased their daily mass gain, but we were not able to detect any statistically significant differences between the treatments in either morning or evening mass. The basis of this apparently contradictory result is fairly straightforward: when birds decrease their morning mass and increase their evening mass, the daily mass gain is the sum of these two changes. Therefore, the daily mass gain

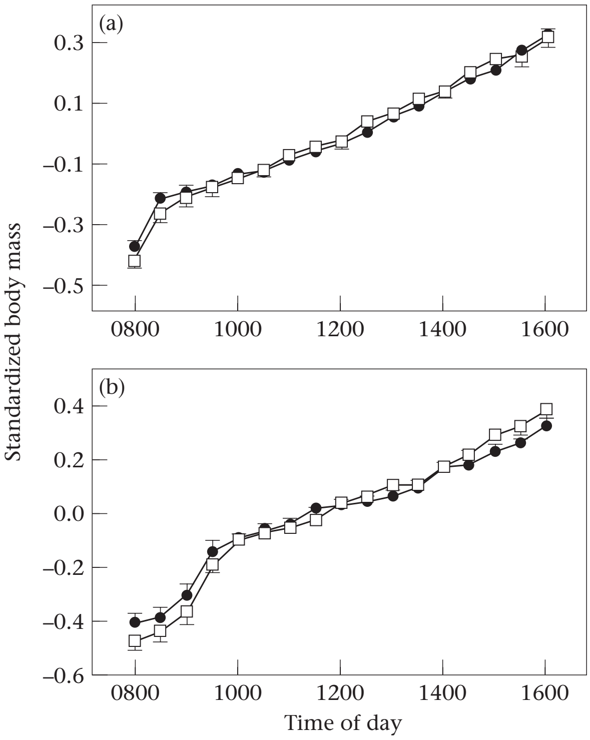

Figure 3. Standardized daily mass patterns (see Methods) of dominant (●) and subordinate (□) flockmates on the ad libitum (a) and limited (b) food schedule. Mass trajectories were standardized to deviations about a daily mean of zero (since dominants are always heavier than subordinates; see Hurly 1992). Vertical lines represent standard errors of standardized means.

may be significantly higher while the change in morning and evening mass would not reach significance.

Both dominants and subordinates under ad libitum access to food gained more mass in the flock than they did when they were solitary. Given that the daily mass gain is evening mass minus morning mass, another way of viewing these differences is that both birds lost more mass at night in the flock (because night mass loss equals morning mass minus evening mass). When birds lose more mass at night, they normally compensate for such a loss by increasing their daily mass gain irrespective of other conditions (e.g. Haftorn 1992). It is not clear why both dominants and subordinates would lose more energy at night when interacting during the day under ad libitum access to food. It is possible that such a change was caused by higher metabolic rates of birds in a flock caused by social interactions (e.g. Røskaft et al. 1986; Cristol 1995). In zebra finches, *Taeniopygia guttata*, dominants gain more mass during the day and lose more mass overnight compared with subordinates (Cuthill et al. 1997). The mechanism for this flock-induced change in

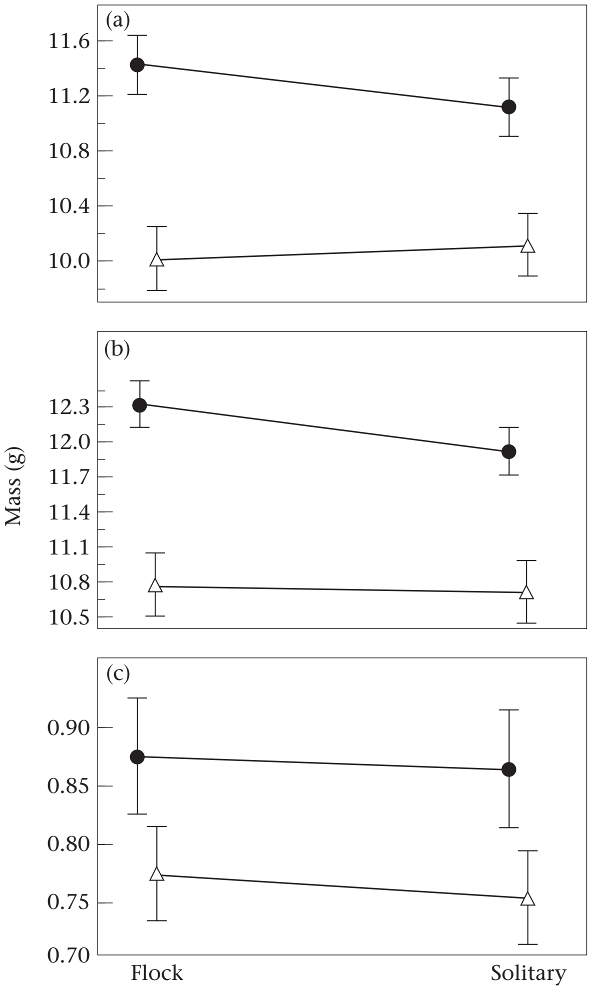

Figure 4. Effect of social dominance on energy reserves in Carolina chickadees on the limited food schedule. Symbols as in Fig. 1.

Table 2. The effect of the treatment (flock versus solitary), dominance status and number of days in the experiment on mass, feeding, food-caching and retrieving rates in Carolina chickadees during the experiment with limited food schedule

	Treatment			Dominance status			Treatment× dominance status			Days in experiment	
Parameter	$F_{1,14}$	P	Power	$F_{1,14}$	P	Power	$F_{1,14}$	P	Power	$F_{1,15}$	P
Morning mass	1.15	0.30	>0.85	16.7	0.001		2.00	0.18	0.62	20.7	<0.001
Evening mass	1.01	0.33	0.81	16.7	0.001		1.46	0.25	0.30	21.2	<0.001
Daily mass gain	0.27	0.61	>0.85	2.1	0.17	>0.85	0.01	0.92	0.61	10.90	0.005
Log (caching rate+1) (seeds/15 min)	1.28	0.28	0.11	0.57	0.46	0.11	0.08	0.79	0.06	2.18	0.16
Log (retrieval rate+1) (seeds/15 min)	2.58	0.13	*	0.03	0.86	*	2.26	0.13	*	0.51	0.49
Log (consumption rate+1) (seeds/15 min)	0.49	0.50	0.78	0.58	0.46	0.78	0.80	0.39	0.28	3.12	0.10

*Within-cell population standard deviation could not be estimated using the SAS REML algorithm.

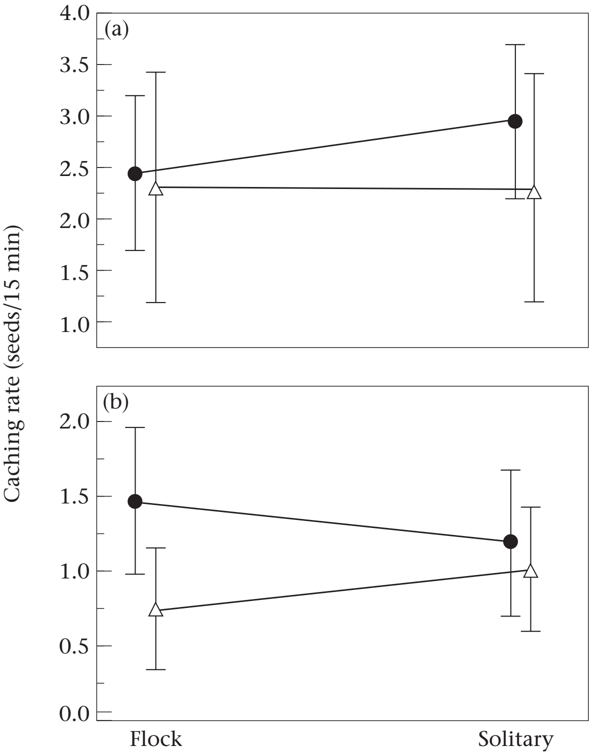

Figure 5. Effect of social dominance on food caching rates in Carolina chickadees on the limited food schedule. Presented are least squares means (means adjusted for covariates) with standard errors (calculated by PROC MIXED: SAS Institute 1994) for dominants (●) and subordinates (△) while in a flock or solitary. (a) Morning; (b) evening.

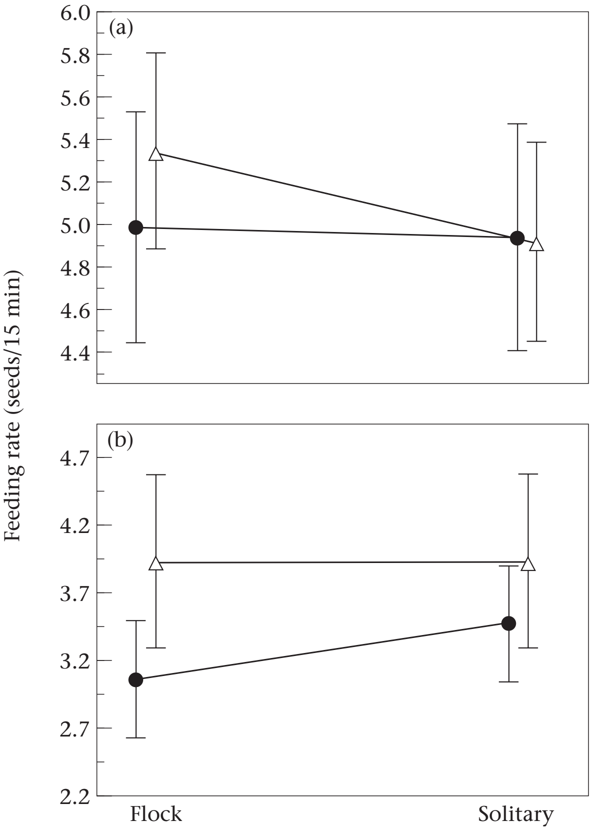

Figure 6. Effect of social dominance on feeding rates in Carolina chickadees on the limited food schedule. (a) Morning; (b) evening. Symbols as in Fig. 5.

diurnal mass pattern in zebra finches is not known. Clearly, we need more data on the effect of social dominance on metabolic rate and on possible mechanisms for such effects to better understand the relationship between social dominance and daily mass gain and nightly mass loss.

If differential energy management is determined by a degree of competition for food in which subordinates are poor competitors (Witter & Swaddle 1995), then it is possible that just two individuals do not provide enough competition to achieve the predicted differences between dominants and subordinates when feeding conditions are favourable (like in our ad libitum food schedule experiment). However, our data suggest that this argument is not correct. Both dominants and subordinates in these flocks gained mass when their mass was compared to their mass under solitary conditions, suggesting that social interactions are sufficient to select for increased mass gain (or a correlated change in activity budget) even under ad libitum access to food.

It is also worth mentioning that the birds in our experiment were maintained in a relatively large space allowing the subordinate some ability to escape dominant aggression, which is almost always the case in nature. In contrast, in the Witter & Swaddle (1995) experiment for example, three European starlings, *Sturnus vulgaris*, were placed in single cages smaller than 1 m^3. Such a small space must have had some effect on birds' aggressive behaviour and perhaps perceived foraging success. In nature, once a subordinate obtains some food, it is likely to be able to get away from a dominant individual. In small experimental spaces this may not be possible. In an experiment by Cuthill et al. (1997), zebra finches ate on a feeder and the feeder was not available to subordinates before the dominants finished eating. In parids, like Carolina chickadees, this is generally not true; birds always fly somewhere to handle food, thus giving other birds time to feed (personal observation). Therefore, in our experiment with the ad libitum food schedule, competition for food did not eliminate the subordinate's access to food, even though a perception of unpredictability of food must have been higher for subordinates. A higher perception of food unpredictability by subordinates should result from a dominant individual's ability to supplant a subordinate from the feeder at any time.

The prediction that dominants and subordinates should differ in their energy management tactics is based on differential access to food (see Witter & Swaddle 1995). Dominants typically have priority of access to food. This reduces the rate at which subordinates can acquire food or it forces subordinates to wait until dominants are sated (Ekman & Lilliendahl 1993). As a result, subordinates are expected to increase their energy reserves strategically as an insurance against potential pitfalls in foraging. However, in contrast to that prediction, in the experiment with the limited food schedule,

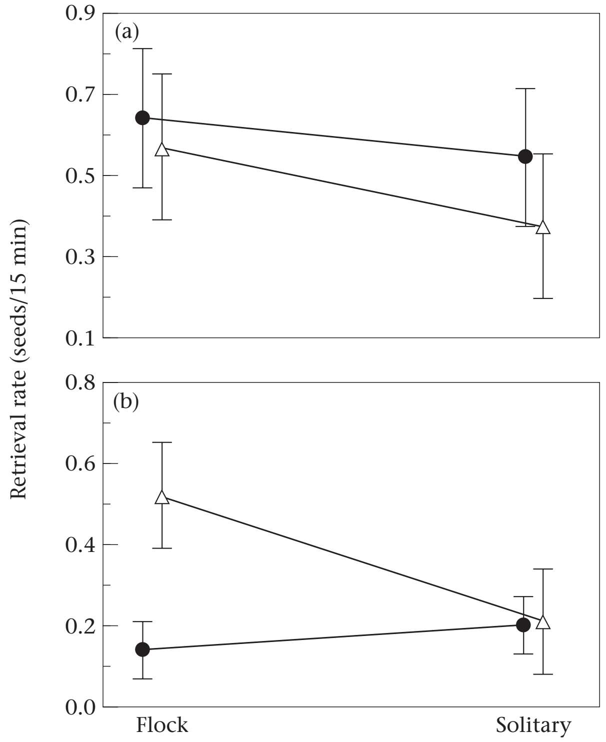

Figure 7. Effect of social dominance on cache retrieval rates in Carolina chickadees on the limited food schedule. (a) Morning; (b) evening. Symbols as in Fig. 5.

dominants were the only individuals that tended to increase their mass when in a flock compared with when solitary.

Verhulst & Hogstad (1996) argued that dominants could maintain higher reserves than subordinates if predation risk for subordinates is higher. In our experiment, the perceived risk of predation was probably the same for both dominants and subordinates. Therefore, the hypothesis of Verhulst & Hogstad (1996) does not provide a reasonable explanation for our results. It is likely that many factors such as food availability and variability, predation risk, presence or absence of safe foraging habitats, flock size and degree of competition might all effect energy reserves in dominants and subordinates when they are in a flock. For example, low availability of food coupled with high variance in foraging may explain why dominant willow tits, *Parus montanus*, in northern Finland carry more fat reserves than subordinate individuals (Koivula et al. 1995), while in central Sweden the same species shows the opposite pattern (Ekman & Lilliendahl 1993).

Daily patterns of mass gain that we observed were strikingly similar between dominants and subordinates both in a flock and when solitary. This suggests that social dominance had no effect on the way the birds were accumulating their energy reserves throughout the day during experiments both with ad libitum and limited food schedules. These results parallel those of Pravosudov & Grubb (1998), who showed that access to cachable food had no significant effect on daily patterns of mass gain, contrary to theoretical predictions (McNamara et al. 1990). The parallel is that cached food should reduce variability in the access to food because a bird can cache when food is relatively abundant and retrieve when food is more scarce. Few birds cached under ad libitum access to food. This result is consistent with previous evidence suggesting that excess food diminishes caching rates (e.g. Lucas et al. 1993). During the experiment with the limited food schedule, all birds regularly cached food. However, in this experiment we failed to detect any statistically significant differences between flock and solitary treatments in caching rates for either dominant or subordinate birds. One possible explanation for such a finding is that in nature birds reduce the possibility of cache pilferage by using special caching tactics like flying a longer distance to cache a food item when in the presence of a dominant individual (Woodrey 1991; Lahti et al. 1998). Thus, under natural circumstances, social conditions may have a limited effect on caching behaviour. However, a study of free-ranging willow tits demonstrated that dominants cached more food compared with subordinates when in a group together, and when the dominants were removed from these groups, the subordinates significantly increased their caching rate (Lahti et al. 1998). Our study found no change in caching rates of either dominants or subordinates between flock and solitary environments in the laboratory. In the laboratory, space is limited and birds in a flock cannot avoid each other when making a cache. Therefore, an increase in cache size may be avoided (even if it would be beneficial otherwise) if caches cannot be concealed from groupmates. However, it is not clear why the chickadees and especially subordinates in our experiments did not have a higher caching rate during the solitary treatment when pilferage was of no concern and a limited food schedule favors more caching (Lucas & Walter 1991; Pravosudov & Grubb 1997).

In conclusion, under ad libitum access to food social interactions in flocks of just two birds caused similar changes in energy management for both dominants and subordinates. When foraging conditions are harsh as in our experiment with the limited food schedule, dominants actually tended to maintain larger fat reserves under flock conditions than under solitary conditions. Finally, the daily pattern of mass gain was similar for both feeding schedules, for both birds in a pair, and under both social conditions. These results support the view of Witter & Swaddle (1995) about a continuum of possible relationships between social dominance and energy reserves.

Finally, several factors could potentially have biased our results. First, because we tested pairs consisting of a male and a female, a pair bond could have formed in the middle of the treatment, despite the fact that both birds were unfamiliar to each other prior to the experiments. However males typically dominate females even in mated pairs (e.g. Ekman & Askenmo 1984; Hogstad 1989). In addition, our behavioural observations showed dominance interactions throughout the experiment and we observed no visual signs of pair formation. These factors argue against a bias caused by a developed pair bond. Second, it is possible that competition for food was not harsh enough under the experimental conditions, because chickadees handle their food away from the feeder. However, this is a natural (not just experimental) pattern of food handling in chickadees. None the less, during our experiments, only one seed was delivered at a time, so birds inevitably had to compete for each seed. At both unlimited and especially limited food schedules, dominants always came to the feeder first and they always supplanted a subordinate if one was there. Thus subordinates did not have free access to food at any time. Instead, they had to adjust to the presence of the dominant, and this probably increased their perception of the variability in access to food. This should be particularly true when food was limited to only 60 min per day. Surprisingly, subordinates failed to gain weight when switched from solitary to flock conditions under limited access to food, but not under unlimited access to food. Coupled with the fact that dominants increased mass under both conditions this argues against this second form of bias: if food was too plentiful or the competition too weak, then no response to social conditions would have been displayed by the birds. Instead, our results suggest that competition was strong enough to elicit a response, albeit a response that failed to meet the prediction. We suggest that more studies are needed to identify the exact conditions that could cause either dominants or subordinates to maintain different energy reserves while in a social environment.

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