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ARTICLES

The effects of energy reserves and dominance on the use of social-foraging strategies in the house sparrow

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In social animals, dominance rank often influences individuals' behaviour, but in most cases it is unknown how dominance modulates the effects of other phenotypic traits. We investigated the mutual effects of social dominance and the level of energy reserves on the use of social-foraging strategies in captive flocks of house sparrows, *Passer domesticus*. We used experimental wind exposure to manipulate overnight energy expenditure of dominant and subordinate individuals. In response to the experimental treatment dominants used scrounging (exploiting others' food finding) significantly more, whereas for subordinates there was only a moderate and nonsignificant increase in scrounging. Individual variability in the frequency of scrounging was higher in subordinates than in dominants and this difference between the dominance groups was unaffected by the treatment. These results suggest that individuals of different dominance status adopt different strategies: to cope with an energetically challenging situation, dominants behave rather uniformly by increasing further their preference for scrounging, whereas subordinates do not alter their tactic, but may rely on using scrounging opportunistically.

Dominance is an important phenotypic attribute of group-living animals: dominant individuals often have superior access to scarce resources, such as mates, food or safe refuges (Huntingford & Turner 1987). This preferential access usually increases the dominants' gain from a given strategy and may constrain the subordinate individuals to use alternative strategies (Gross 1996). Although there is considerable evidence for these dominance effects, our knowledge of how these effects interact with other phenotypic attributes is limited.

Another phenotypic characteristic that is crucial for animals' decision making is the level of energy reserves. In contrast to dominance rank, which remains relatively stable across long periods (weeks or even years), the level of energy reserves may show significant daily variation (Broggi et al. 2003). Thus, as the level of energy reserves changes during the day, the animal's dominance status and actual physical state may favour different behavioural responses: for example, low levels of energy reserves would favour the use of a particular foraging tactic while the dominance status of the individual may favour another one. How then should an animal adjust its strategy to such multiple demands of its phenotypic state?

This question has rarely been investigated in a social context, that is, when the payoff from an individual's decision depends also on the behaviour of its companions. We investigated how dominance rank modulates the effects of the level of energy reserves in social strategy use of house sparrows, *Passer domesticus*. Social foraging is one of the best studied systems, where animals may use distinct alternative tactics in a group of interacting individuals. Individuals may either search for food on their own ('producing') or join their feeding companions and exploit their food discoveries ('scrounging'). Individuals

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of many species use these tactics in a flexible way: for instance, birds may frequently switch between producing and scrounging according to current ecological conditions or to their own internal state (e.g. Koops & Giraldeau 1996; Coolen 2002; Liker & Barta 2002; Barta et al. 2004; Lendvai et al. 2004).

Liker & Barta (2002) showed that the tactic used during social foraging is related to dominance rank in the house sparrow; dominant individuals use scrounging more than subordinates do. Furthermore, the level of energy reserves also influences tactic choice: individuals with low energy reserves use scrounging more than individuals with high levels of reserves do (Lendvai et al. 2004). However, in the latter study we controlled for the effects of dominance and investigated only the behaviour of middle-ranked birds. In the present study, we analysed the mutual effects of dominance rank and energy reserves: by using experimental manipulation we investigated the effects of energy reserves on the social-foraging behaviour of high- and low-ranking individuals.

METHODS

Study Subjects

We captured 88 house sparrows with mist nets between 8 November 2002 and 10 February 2003 in Budapest, Hungary, and in two neighbouring villages, Dunakeszi and Üllő. From these we formed four captive flocks, each with 22 individuals. Four birds died before the experiments, for unknown reasons (we found no evidence of physical injuries or infections on dead birds). Wild-caught birds may die in captivity if they are particularly susceptible to handling or a changing and potentially stressful environment (Gonzalez et al. 1999). Nevertheless, the survival of birds in our study flocks during the approximately 1 month of captivity was high (95.5%) compared to other studies on captive house sparrows (e.g. 63% during 3 months: Gonzalez et al. 1999; 64% during 2 weeks: Gill & Paperna 2005). After the death of the four birds, our flocks included 19, 22, 22 and 21 individuals, respectively, and these flock sizes did not change further. Sex ratio in the flocks was approximately balanced (10:9, 13:9, 11:11 and 12:9 males:females, respectively). After capture we measured body mass (±0.1 g), tarsus (±0.1 mm) and wing length (±1 mm), and ringed all birds with a numbered metal ring and three colour rings.

After the measurements, the birds were taken to an 'acclimatizing' aviary (2 × 3 m and 2 m high), where they were kept for at least 1 week to become familiar with the experimental environment. Before we started the observations (see below) the flocks were transferred to a 'test' aviary, (3 × 4 m and 2 m high), while another flock was captured and placed in the acclimatizing aviary. All observations (i.e. data collection on fighting behaviour and on foraging tactic use) were carried out in the test aviary, where the birds spent 2 weeks. The two aviaries were separated so that individuals of different flocks could not interfere with each other.

Both aviaries were lit by artificial light with 9:15 h light:dark periods and contained artificial roosting trees and several small (10 × 10 × 10 cm) boxes for sleeping and resting. The aviaries also contained two water dishes, two sand dishes and one dish with pieces of fine gravel to facilitate digestion. Feeding took place on a 1.2 × 1.2-m plywood board ('grid' henceforth) that contained a 12 × 12 grid of 144 equidistant wells (diameter: 2.5 cm; depth: 1.2 cm) for presenting food. Water and food were provided ad libitum during acclimatization and between observations. Food consisted of millet, oat, wheat, hemp and sunflower seeds. In addition, multivitamin droplets were added to the water. Birds apparently became familiar with the aviaries during both the acclimatization period and the first week in the test aviary and they had learned to use the grid to search for food by the time we observed foraging behaviour in the second week (see below). We observed all individuals foraging from the grid; thus the presence of dominants did not prevent the subordinates from feeding. Birds maintained their body mass during their time in captivity (at capture: $\overline{X} \pm \mathrm{SE} = 28.53 \pm 0.53$ g; after the observations: 28.19 ± 0.32 g; paired *t* test: $t_{43} = 0.146$, $P = 0.884$).

After the experiment, birds were released at the site of capture. Released birds probably re-established themselves in the local colony, as we often subsequently encountered them at the capture sites (A. Z. Lendvai, personal observation). The study was licensed by the Duna-Ipoly National Park.

Experimental Protocol

The experiment consisted of two parts for each flock. First, as we intended to study the effect of energy reserves in dominant and subordinate birds, we categorized birds into dominance groups according to their success in aggressive interactions. We observed behaviour, with binoculars, through one-way windows. We conducted observations for 5–7 days for each flock and recorded fights between pairs of individuals. We began the observations in the morning and observation periods lasted 4–6 h/day. We recorded a mean ± SE of 423 ± 48 dyadic fights/flock. For each individual in a flock, we determined fighting success (number of fights won from the total number of fights in which an individual was involved; for more details see Liker & Barta 2001, 2002). An individual was considered to win a fight if he or she clearly supplanted the opponent. The intensity of fights varied from simple displacements to aerial fights. The aviary provided enough space for the birds to retreat from aggressive encounters and during the observations we detected no visible injuries (e.g. plucked feathers or cases of bleeding). We ranked individuals within each flock based on their fighting success (as fighting success correlates strongly with dominance rank, Liker & Barta 2001) and divided them into three dominance categories: dominants, subordinates and middle-ranked birds (Lendvai et al. 2004). Dominants were the six highest-ranked individuals in flocks with 22 birds, and the five highest-ranked individuals in flocks with 21 and 19 birds. Similarly, individuals with the six lowest ranks were considered as subordinates in the flocks with 22 birds, and five and four individuals with the lowest ranks in flocks with 21 and 19 birds, respectively. Then we used the dominants and the subordinates in each flock as the subjects of the manipulation (see below).

In the second part of the experiment, we manipulated the overnight energetic expenditure of dominant and subordinate birds, and then observed their foraging behaviour during their first foraging next morning. In the evening prior to the foraging observations, we captured all birds and removed all food items from the aviary. Middle-ranked birds were immediately released back to the aviary to form the 'core flock' (sensu Giraldeau et al. 1994). After weighing the dominants and subordinates, we individually housed them in cages measuring 0.3 × 0.4 m and 0.6 m high. Half of the dominants and half of the subordinates were randomly assigned to the manipulation, whereas the remainder were controls. In flocks with five individuals, we randomly allocated the fifth bird to the manipulation or the control treatment.

To manipulate overnight energy expenditure, we placed an electric fan in front of the cage of each manipulated bird to simulate wind exposure, whereas controls were kept in the cages without wind exposure (see also Lendvai et al. 2004). Fans operated throughout the night (15 h). Ambient temperature during the treatments was 12–16°C. All cages were in the same room, so the noise disturbance was similar for all birds. Wind exposure has been successfully used to manipulate overnight energy expenditure (Cuthill et al. 2000; Lendvai et al. 2004).

The next morning, 1 h before lights on, the birds were removed from their cages and weighed again. Then they were released back to the core flock in the aviary and were left there undisturbed for at least 30 min to recuperate. At lights on, we placed millet seeds in 12 randomly chosen wells on the grid (approximately 120 seeds per wells). After the provision of food, we recorded the behaviour of the birds with two synchronized digital video cameras through one-way windows approximately 2 m from the grid (for further details see Lendvai et al. 2004). We used the video recordings to analyse behaviour. Feeding trials lasted 5 min, during which seed clumps were usually depleted and the birds left the grid. After the trials, food containers were replenished ad libitum.

Data Processing and Statistical Analyses

We analysed the foraging behaviour of the 22 dominant and 22 subordinate sparrows from the four flocks (11 experimental and 11 control birds in both dominance categories). We followed each experimental and control bird throughout the trial on the video recordings and coded their behaviour. We also recorded the time when the birds arrived on the grid, and their time spent on the grid. The behaviour of unmanipulated middle-ranking individuals (the 'core flock') was not analysed (see also Giraldeau et al. 1994). Although each individual's behaviour depends on that of the other birds in the flock, the presence of the core flock individuals means that the behaviour of the experimental individuals is not directly dependent on that of other experimental individuals, preserving the statistical independence of data points.

Feeding events were divided into two types, finding and joining. In finding events a bird discovered an unoccupied well (i.e. no other birds were within 10 cm of the well) and fed from it. In joining events the well from which the focal bird fed was occupied by another feeding bird at the moment the focal individual arrived. We calculated joining proportion as the number of all joining events divided by the total number of feeding events (i.e. number of finding plus joining events) of each focal bird during the trial. This proportion was used as a surrogate of scrounger tactic use (Beauchamp 2001; Barta et al. 2004). We measured the variability of joining proportion in each treatment group for both dominance ranks. To do this, we calculated the absolute differences of individual joining proportions from the median joining proportion within the four categories (i.e. for the two dominance × two treatment groups separately). We also measured the proportion of all joining attempts: the number of successful plus unsuccessful joining attempts divided by the number of all food-searching attempts (i.e. finding plus unsuccessful searching; Lendvai et al. 2004). Finally, we measured overall food intake as the total number of pecks during the trial, and overall feeding rate as the total number of pecks divided by the time spent on the grid. These measures of overall food intake and feeding rate included pecks from both found and joined patches.

We analysed our data by linear mixed-effects models, with flock as a random factor. The effect of flock, however, was nonsignificant in most cases; therefore we do not present statistical results for nonsignificant flock effects. Two-tailed probabilities and mean ± SEs are given throughout the paper. We used SPSS 11.0 (SPSS Inc., Chicago, IL, U.S.A.) for statistical analyses.

RESULTS

Overnight Body Mass Change

Neither dominance groups nor treatment groups differed in body size measured at capture (body size measured as tarsus length and wing length; MANOVA: dominance group: Wilk's $\lambda_{37} = 0.975$, $P = 0.625$; treatment: Wilk's $\lambda_{37} = 0.992$, $P = 0.868$). There was also no difference between dominance and treatment groups in the premanipulation (evening) body mass (dominance group: $F_{1,38} = 0.093$, $P = 0.763$; treatment: $F_{1,38} = 2.264$, $P = 0.141$). The overnight decrease in body mass during the night of treatment differed between flocks ($F_{3,37} = 9.805$, $P < 0.001$). However, as expected, it was greater in wind-exposed than in control groups, whereas it was similar in high- and low-ranked birds, with no interaction between dominance and treatment (dominance group: $F_{1,37} = 1.148$, $P = 0.291$; treatment: $F_{1,37} = 5.677$, $P = 0.022$; dominance group * treatment interaction: $F_{1,37} = 0.162$, $P = 0.690$; Fig. 1). This overnight decrease was on average $10.3 \pm 0.36\%$ of evening body mass, but only the flock and the experimental treatment had an influence on the percentage of body mass lost (flock: $F_{3,37} = 13.4944$, $P < 0.001$; dominance group: $F_{1,37} = 1.274$, $P = 0.266$; treatment: $F_{1,37} = 5.152$, $P = 0.029$; dominance group * treatment interaction: $F_{1,37} = 0.576$,

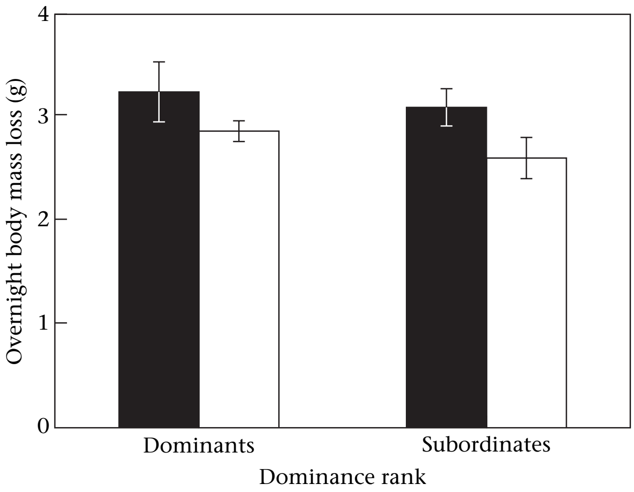

Figure 1. Mean ± SE overnight body mass loss (g) of house sparrows in relation to dominance group and treatment ($N = 44$ individuals, with 11 wind-exposed (■) and 11 control (□) individuals in both the dominant and subordinate groups).

$P = 0.453$). Larger birds tended to lose more of their evening body mass than smaller ones; however, the treatment had a significant effect on overnight body mass loss even after we controlled for body size (flock: $F_{3,36} = 14.023$, $P < 0.001$; tarsus: $F_{1,36} = 2.885$, $P = 0.098$; dominance group: $F_{1,36} = 1.897$, $P = 0.177$; treatment: $F_{1,36} = 4.448$, $P = 0.042$; dominance group * treatment interaction: $F_{1,36} = 0.496$, $P = 0.486$).

Foraging Behaviour

Birds in the four experimental groups showed a large variability in terms of tactic use: the observed joining proportion ranged from zero to one (Fig. 2). Variability in joining proportion was greater in the subordinate groups than in the dominant groups, but the treatment had no influence on the variability (dominance group: $F_{1,37} = 10.150$, $P = 0.003$; treatment: $F_{1,37} = 0.372$, $P = 0.546$; dominance group * treatment interaction: $F_{1,37} = 0.001$, $P = 0.979$; Fig. 2). Owing to this significant heteroscedasticity, we could not analyse the two dominance groups together, because one of the main assumptions of the ANOVA model (the homogeneity of variances) would be violated. Variable transformations did not resolve this heteroscedasticity in the data.

In the dominant group, in response to the wind exposure, individuals increased their use of joining, whereas in subordinates we found no difference between experimental groups (dominants: treatment: $F_{1,17} = 15.398$, $P = 0.001$; subordinates: treatment: $F_{1,17} = 0.806$, $P = 0.382$). The treatment had no effect on joining attempts (dominants: treatment: $F_{1,17} = 4.061$, $P = 0.060$; subordinates: treatment: $F_{1,17} = 1.502$, $P = 0.237$); however, within the dominant group, wind-exposed birds tended to make more attempts at joining than control birds did (wind-exposed versus control means with 95% confidence interval: 0.486, 0.354–0.618 versus 0.323, 0.191–0.455), whereas in subordinate individuals the difference in joining attempts between wind-exposed and control treatments was smaller (0.348, 0.216–0.480 versus 0.223, 0.090–0.355).

Experimental treatment did not affect the number of food patches (i.e. wells) found by the birds in either group (Table 1). Overall feeding rate, overall food intake and time spent on the grid also did not differ between experimental treatments in either group (Table 1).

DISCUSSION

In this study we investigated the mutual effects of dominance rank and energy reserves on social-foraging

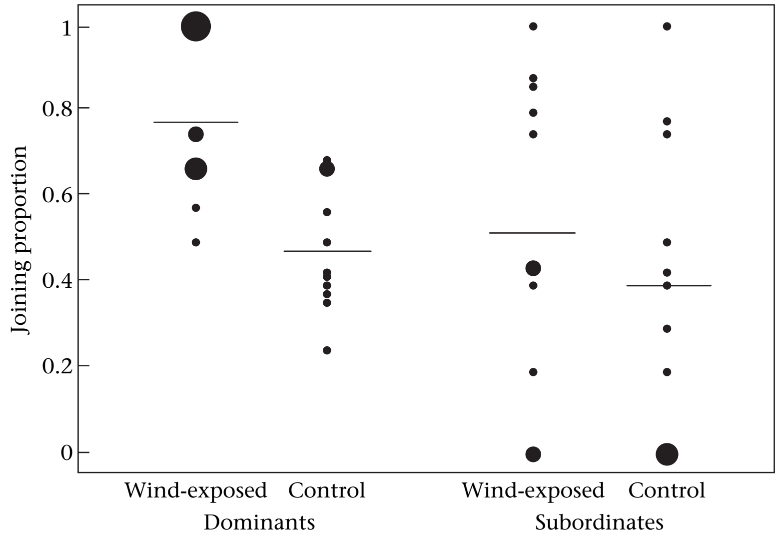

Figure 2. The distribution of joining proportion (the number of feeding events where the focal bird joined another feeding individual divided by the total number of feeding events) in relation to dominance group and treatment. The size of the dots indicates the number of individuals (1, 2, 3 or 4) with identical joining proportion values. $N = 44$ individuals, with 11 wind-exposed and 11 control individuals in both the dominant and subordinate groups. Horizontal lines indicate the means for each group.

Table 1. The effect of dominance rank and wind exposure on foraging behaviour (ANOVA, with flock as random factor and treatment as fixed factor)

	Effect of wind exposure			
	Dominants		Subordinates	
Response variable	$F_{1,17}$	P	$F_{1,17}$	P
Time spent on the grid	0.538	0.473	0.500	0.489
Number of food patches found	0.008	0.932	0.107	0.748
Feeding rate	0.070	0.795	0.806	0.382
Food intake	0.002	0.964	1.699	0.210

Nonsignificant flock effects are not shown.

behaviour. We found that in response to the wind exposure both dominance groups tended to increase the proportion of joining. However, this increase was significant only in the dominant group. The increase in the proportion of joining was 2.5 times greater in the dominant group than in the subordinate one.

This difference between the dominance groups may have several explanations. First, it could be a consequence of a greater effect of wind exposure on dominant individuals. Nevertheless, we found no effect of dominance on overnight body mass loss after the wind exposure, and the mean difference between wind-exposed and control individuals was even slightly greater in subordinates (0.49 g) than in dominants (0.38 g). Second, reducing energy reserves might increase attempts at scrounging in both dominance groups but subordinate sparrows might be unable to scrounge effectively because of the increased scrounging activity of dominants. The payoff from scrounging is frequency dependent, that is, its frequency in a group cannot be increased beyond a certain point (Barnard & Sibly 1981; Giraldeau & Livoreil 1998). However, this explanation is also unlikely, because apart from the frequency of successful joining, wind-exposed subordinates did not increase the frequency of their joining attempts either.

A more likely explanation for the different effect of wind exposure may be that individuals of different dominance rank adopt different strategies, that is, the same change in energy reserves generates different behavioural reactions in terms of tactic use in high- and low-ranked birds. In response to the wind exposure dominant individuals showed a marginally nonsignificant trend to initiate more joining and made significantly more successful joining attempts. These results suggest that when energy reserves of dominant individuals are low, they both increase their preference for joining and become more successful. This is not surprising, since house sparrows are often aggressive when scrounging (Johnston 1969; Liker & Barta 2002), and hungry sparrows may be more motivated and more successful in fights than their more satiated companions (Andersson & Åhlund 1991). In contrast, within the subordinate group, we found only a moderate and nonsignificant difference between the treatment groups in both the proportion of all joining attempts and the proportion of successful joining events. The latter result suggests that subordinates are not simply less successful at joining than dominants, but that their behavioural response to the change in level of energy reserves is different from that of dominants. This might be explained by the fact that being subordinate reduces the chances of successfully supplanting other sparrows from a discovered patch (e.g. Wiley 1991). Hence, energetically stressed subordinates, instead of increasing the use of scrounging, must cope with this situation by other means.

Further evidence for the dissimilarity in strategy use between the dominant and subordinate birds is the difference in the variability of the joining proportions between the high- and low-ranking individuals. This difference was unaltered by the experimental treatments, that is, this heterogeneity in the variability of tactic use was explained only by the differences in dominance rank. But why does this variability differ between dominant and subordinate individuals? Subordinates might find fewer food patches, and consequently the calculation of their joining proportion would have a higher error. This explanation is unlikely, however, as the difference in the variance of joining proportion between dominance groups remained significant after we controlled for the number of food patches found (results not shown).

The difference in the variance of joining proportion is more likely to indicate that individual differences in tactic use are greater in subordinates than in dominants. Dominants use the joining tactic frequently (Liker & Barta 2002), but when their energy reserves fall, they can still increase their use of joining, mainly by using aggression. Since dominant birds have a clear advantage in aggressive interactions (i.e. they win more fights), they can increase their use of scrounging; for some individuals it may even be possible to use scrounging exclusively (e.g. see the four individuals with the highest joining proportion in the wind-exposed dominant group in Fig. 2). On the other hand, subordinates may be predisposed to use mainly the producing tactic (Barta & Giraldeau 1998), but they may follow an opportunistic strategy: they may scrounge whenever they have an opportunity to do so. For example, since house sparrows aggressively defend food patches, attempting to scrounge from a high-ranking individual would entail costs of time, energy and the risk of injury for a subordinate bird. Consequently, tactic choice of subordinates may be more context dependent than that of dominants, that is, it may be more influenced by the actual circumstances (e.g. by the dominance rank of the surrounding patch owners). Owing to this context dependence, some 'lucky' subordinate individuals may scrounge frequently, while others may lack the opportunities and use mainly the producing tactic. Our results are consistent with those from a study on great tits, *Parus major*, showing that dominant individuals are likely to form consistent foraging routines, whereas subordinate individuals cautiously adjust their behaviour to changes in the environment (Drent & Marchetti 1999).

In both dominance groups, feeding rate and overall food intake did not differ between the treatment groups. This result is consistent with our previous studies, where we found that tactic use was unrelated to the food reward (i.e. feeding rate; Liker & Barta 2002; Lendvai et al. 2004). However, we investigated only the birds' first foraging during the day, where food resources were quickly depleted. In a natural environment individuals feed many times in a day and may recover their body mass later on. Recent dynamic models suggest that early in the morning birds tend to maximize their immediate survival prospects, and mass gain becomes more important later in the day (Barta & Giraldeau 2000). As a result, by determining the level of scrounging use, animals may principally regulate the risk of an energetic shortfall and trade it off against the costs of scrounging, such as energetic costs and risk of injury.

To summarize, our study has provided the first experimental investigation on the mutual effects of multiple state variables on the use of tactics during social foraging. We have shown that the effects of dominance modulate the effects of energy reserves: a low level of energy reserves status reinforces a preference for scrounging in high-ranking individuals, whereas it generates only a weak preference for scrounging in subordinate birds. Thus dominance status may determine what behavioural alternatives are available for animals in an energetically challenging situation. If dominant individuals have a wider range of available behavioural actions in such situations, they may have an advantage in choosing the optimal strategy. This interesting benefit of being dominant would be worth investigating further in the future.

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