

The effect of energy reserves on social foraging: hungry sparrows scrounge more

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Animals often use alternative strategies when they compete for resources, but it is unclear in most cases what factors determine the actual tactic followed by individuals. Although recent models suggest that the internal state of animals may be particularly important in tactic choice, the effects of state variables on the use of alternative behavioural forms have rarely been demonstrated. In this study, using experimental wind exposure to increase overnight energy expenditure, we show that flock-feeding house sparrows (*Passer domesticus*) with lowered energy reserves increase their use of scrounging (exploiting others' food findings) during their first feed of the day. This result is in accordance with the prediction of a state-dependent model of use of social foraging tactics. We also show that scrounging provides less variable feeding rates and patch finding times than the alternative tactic. These latter results support the theoretical assumption that scrounging is a risk-averse tactic, i.e. it reduces the risk of immediate starvation. As the level of energy reserves predicts the use of social foraging tactics, we propose that selection should favour individuals that monitor the internal state of flock mates and use this information to adjust their own tactic choice.

Keywords: producer–scrounger game; state-variables; starvation risk; foraging strategies; house sparrow; *Passer domesticus*

1. INTRODUCTION

Animals often follow alternative behavioural tactics when they compete for resources such as mates or food (Maynard Smith 1982; Gross 1996; Giraldeau & Caraco 2000). Although the evolutionary outcomes of behavioural polymorphism can be explained by theoretical models (Maynard Smith 1982; Gross 1996; Houston & McNamara 1999; Giraldeau & Caraco 2000), we know less about what factors actually determine the tactic followed by an individual in a particular situation. Recent models suggest that the state of individuals, such as age, size, level of energy reserves or parasite load, can effectively influence what actions are available to them and how these actions affect their fitness (Gross 1996; Houston & McNamara 1999). Consequently, the internal state of animals can significantly determine their choice between alternative behavioural tactics (Houston & McNamara 1987, 1988, 1999). Experimental tests of the effects of state variables on tactic use, however, are scarce.

Social foraging is one of the best-studied systems where individuals use alternative tactics (Giraldeau & Caraco 2000). For instance, in flock-feeding birds it is frequently observed that some individuals (producers) actively search for food patches whereas others (scroungers) wait for producers to discover a patch and then feed from it (Barnard & Sibly 1981; Giraldeau & Caraco 2000). It has been shown that individuals of many species flexibly use these tactics,

i.e. birds may frequently switch between producing and scrounging (e.g. Koops & Giraldeau 1996; Coolen *et al.* 2001; Liker & Barta 2002). Although the results of several studies suggest that the frequency of scrounging may be related to ecological factors (e.g. food distribution, Koops & Giraldeau 1996; predation risk, Barta *et al.* 2004) and the birds' phenotypes (e.g. age, Steele & Hockey 1995; dominance rank, Liker & Barta 2002), the effects of quickly changing state variables on tactic use are poorly understood.

It is widely accepted that the level of energy reserves might be a particularly important state variable that can affect the use of social foraging tactics. In a state-dependent dynamic game model, Barta & Giraldeau (2000) investigated the effects of energy reserves on the frequency of scrounging. This model, in which the effects of the individuals' dominance ranks were not considered, predicts that when an individual faces an energy shortfall (i.e. when its energy reserves are near to its lower lethal boundary) it is optimal to be risk-averse, i.e. to follow a tactic that minimizes the risk of immediate starvation by providing a small but reliable amount of food. Risk-sensitive models of social foraging propose that scrounging is a risk-averse tactic, because individuals can decrease the variance in their food intake by increasing the use of scrounging (Caraco & Giraldeau 1991; Barta & Giraldeau 2000). Consequently, Barta & Giraldeau's (2000) model predicts that, early in the morning, birds with low energy reserves will increase the use of scrounging, whereas individuals with high reserves will more often be producers. Note that this prediction is different from the energy budget rule (Stephens 1981) which does

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not consider the possibility of immediate starvation and predicts risk-prone behaviour if the animal cannot meet its daily energy requirement (i.e. it has low reserves).

In this study we investigated the effects of energy reserves on the use of social foraging tactics in house sparrow (*Passer domesticus*) flocks. Sparrows usually feed in flocks and use both producer and scrounger tactics to find their food (Barnard & Sibly 1981; Johnson *et al.* 2001; Liker & Barta 2002). To investigate the effects of energy reserves we experimentally manipulated the birds' overnight energy expenditure by simulating nocturnal wind exposure. We tested the specific prediction of Barta & Giraldeau's (2000) model that individuals with lowered energy reserves should use scrounging more frequently than control birds early in the morning. Furthermore, we investigated one of the basic assumptions of the model, namely that scrounging is risk-averse, i.e. it provides more reliable rewards than producing for individuals trying to avoid starvation early in the day.

2. MATERIAL AND METHODS

(a) *Study subjects*

We captured 88 house sparrows with mist nets between 8 November 2002 and 10 February 2003 in Budapest and then formed four flocks, each consisting of 22 individuals. Some of the birds died before the experiments; thus our flocks comprised 19, 22, 22 and 21 individuals during the experiments. The 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. We also marked the individuals with small dye spots on their crown or tail feathers to facilitate quick individual recognition during the observations.

After the measurements the birds were taken to a 2 m (W) \times 3 m (L) \times 2 m (H) 'acclimatizing' aviary, where they were kept for at least one week to become familiar with the experimental environment. The flocks were then transferred to a 3 m (W) \times 4 m (L) \times 2 m (H) 'test' aviary, while another flock was captured and placed in the acclimatizing aviary. All observations (i.e. data collection on fighting behaviour and testing foraging tactic use) were performed in the test aviary, where the birds spent two 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 (9L:15D) and contained artificial roosting trees and small boxes for sleeping and resting. Water, sand and fine gravel (to facilitate digestion) were provided *ad libitum*. Feeding took place on a 1.2 m \times 1.2 m plywood board ('grid' henceforth) that contained a 12 \times 12 grid of 144 equidistant wells (diameter 2.5 cm, depth 1.2 cm) for presenting food (Liker & Barta 2002; Barta *et al.* 2004). The birds were provided with millet, oat, wheat, hemp and sunflower seeds *ad libitum* during the acclimatization period and between observations. In addition, multi-vitamin droplets were added to their water. The birds apparently became familiar with the aviaries during the acclimatization period and subsequent observations on fighting behaviour (see below), and they had learned to use the grid actively to search for food by the time of the experimental testing of foraging behaviour.

After the experiment, the birds were released at the site of capture. Released birds were in good condition and appeared to re-establish themselves in the local colony, as we often re-encountered them at the capture sites (Á.Z.L., personal

observation; Liker & Barta 2001). The study was licensed by Duna-Ipoly National Park (847/3/2003).

(b) *Experimental protocol*

The experiment consisted of two parts for each flock. First, because scrounging sparrows are often aggressive against flock mates and dominance status influences the foraging tactics of individuals (Liker & Barta 2002), we attempted to reduce dominance effects by using 'middle-ranked' individuals in the experiments. To do so, we observed fighting behaviour for one week in each flock. Fighting observations were only recorded when the birds were feeding on the grid. During the observations we recorded 1695 fights between pairs of individuals (mean \pm s.e.m.: 423 \pm 48 fights per flock). For each individual in a flock, we determined fighting success (number of fights won per total number of fights in which an individual was involved; for more details see Liker & Barta 2001, 2002). We ranked individuals within each flock on the basis of their fighting success (as fighting success strongly correlates with dominance rank; Liker & Barta 2001) and selected the ten middle-ranked individuals in each flock (starting from rank 7 in the flocks with 22 birds, and from rank 6 in the flocks with 19 and 21 birds). We then used the 10 selected birds per flock as the subjects of the manipulation (below).

In the second part of the experiment we manipulated the middle-ranked birds' overnight energy expenditure and then observed their foraging behaviour during their first foraging next morning. In the evening before the foraging observations, we captured all birds and removed all food items from the aviary. High- and low-ranked birds were immediately released back to the aviary to form the 'core flock' (Giraldeau *et al.* 1994). After measuring the body mass (± 0.1 g) of the middle-ranked birds we housed them individually in cages measuring 0.3 m (L) \times 0.4 m (W) \times 0.6 m (H). Half of these birds were randomly assigned to the manipulation, whereas the remainder were controls (i.e. 5:5 individuals in each flock). To manipulate overnight energy expenditure we placed electric fans in front of the cages of each manipulated bird to simulate wind exposure, whereas controls were kept in the cages without wind exposure. Fans operated throughout the night. Ambient temperature during the treatments ranged from 12 to 16 °C. To prevent air flow across the cages, we placed plastic sheets (0.7 m \times 0.5 m) between them. In addition, we placed two 1.5 m \times 1 m plastic sheets on both sides of each fan and one sheet above these, to avoid air turbulence in the room as much as possible. All cages were located within the same room, so the noise disturbance was similar for all birds. Wind exposure significantly reduces surface body temperature and increases metabolic rate in small passerines (Bakken & Lee 1992; Wolf & Walsberg 1996; Zerba *et al.* 1999), and has been successfully used to manipulate overnight energy expenditure (Witter *et al.* 1994; Cuthill *et al.* 2000). One might argue that restricted access to food could be a more effective means of reducing reserves. Food deprivation would, however, not only decrease the birds' energy reserves but also change their estimation of food variability and predictability, both of which are considered to affect foraging behaviour (Cuthill & Houston 1997; Houston & McNamara 1999; Cuthill *et al.* 2000). To avoid these confounding changes in foraging we manipulated overnight wind exposure only.

The next morning, one hour before lights on, the birds were removed from their cages and their body mass was measured again. They were then released back to the core flock in the aviary and were left there undisturbed for at least 30 min to reassure themselves. At lights on, we placed millet seeds in 12 randomly chosen wells on the grid (approximately 120 seeds per well). After

the provision of food, we started to record the behaviour of the birds with two synchronized digital video cameras through one-way windows approximately 2 m from the grid. One video camera was fixed on a tripod and filmed the whole grid, while the other camera was controlled by the observer and was used to take close-up pictures of the individuals on the grid so that their individual markings were unambiguously recognizable. Because the cameras were synchronized and the wells were numbered to recognize position, we could use close-up recordings to identify individuals on the other ('whole-grid') records which were used to analyse behaviour. Feeding trials lasted 5 min, during which seed clumps were usually depleted and the birds left the grid.

(c) Data processing and statistical analyses

We analysed the foraging behaviour of 40 middle-ranked sparrows (20 experimental and 20 control) from the four flocks. We followed each experimental and control bird throughout the trial on the whole-grid video record and coded their behaviour. We also recorded the time when the birds arrived on the grid, and their time spent on the grid.

Feeding events were divided into two types, finding and joining. These terms were used instead of producing and scrounging, respectively, because we recorded actual feeding events and not directly observed tactic use, i.e. whether a bird was searching as a producer or a scrounger (Mottley & Giraldeau 2000; Coolen *et al.* 2001; Liker & Barta 2002). In 'finding' events a bird discovered an unoccupied well (i.e. no other birds 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 of the arrival of the focal individual. 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) for each focal bird during the trial. This proportion was used as a surrogate of scrounger tactic use. Note that one bird left the grid without feeding; thus this individual was omitted from the analysis of joining proportions.

We also recorded joining attempts, i.e. the number of unsuccessful attempts to obtain food either by attacking foraging individuals or 'stealing' food items by quick pecks from an occupied well. Furthermore, we recorded the number of food searching attempts: we defined birds' behaviour as an attempt at food searching when they clearly looked into a well, e.g. with quick glances into the well with characteristic side-turned head position, or by popping the head into the hole. Similarly to joining proportion, we calculated joining attempt proportion, which was the number of joining attempts divided by the total number of attempts (i.e. joining attempts plus food searching attempts). Finally, we measured overall feeding rate as the total number of pecks divided by the time spent on the grid. This measure of feeding rate included pecks from both found and joined patches.

To compare the variability and success of the two feeding tactics, we recorded the following variables for each feeding event: (i) the tactic by which the food patch (i.e. well) was discovered; (ii) patch-finding time as the time elapsed from leaving the previous well from which the bird fed until the start of the given feeding event. In the case of the first well, this value was the time elapsed from arrival at the grid until the first successful feeding event. We also measured: (i) the time spent in the patches, i.e. the time elapsed from acquiring the well containing food until leaving it; and (ii) the number of food items eaten from the well. From these variables we calculated the patch feeding rate, i.e. the number of pecks from the given patch divided by the patch-finding time plus the time spent in that patch (Stephens & Krebs 1986). Note that this calculation

assumes that time spent searching between patches can be clearly assigned to joining or finding, i.e. the birds do not change tactic during a search.

We estimated the within-individual variability of patch feeding rates for each tactic as absolute differences from the average patch feeding rates, where average patch feeding rates were calculated within individuals for each tactic separately. The variability in patch finding times was similarly estimated. Differences were log-transformed and analysed by parametric tests. To compare the success of the different tactics we compared the within-individual average patch feeding rates between tactics.

Biometric variables were analysed by a MANOVA model with treatment as a fixed factor and flock as a random factor. We used the same model structure in an ANOVA model to analyse changes in body mass. Foraging behaviour data were analysed by linear mixed effect models ('lme' function of the 'nlme' package of the R statistical computing environment; Pinheiro & Bates 2000) with flock as the random factor. Where distributional assumptions of 'lme' did not hold we used 'glm' with binomial error. The effect of flock was, however, non-significant in all cases; therefore we do not present statistical results for flock effects. Two-tailed probabilities and mean \pm s.e.m. are given. We used the R statistical computing environment (R Development Core Team 2003) and SPSS for Windows v. 8.0 for statistical analyses.

3. RESULTS

(a) Body mass change

Individuals in the wind-exposed and control groups did not differ in body size measured at capture (tarsus length, wing length and body mass; MANOVA, treatment: Wilks' $\lambda = 0.965$, d.f. = 33, $p = 0.752$) or in fighting success (ANOVA, treatment: $F_{1,35} = 0.194$, $p = 0.663$). There was also no difference between the two groups in the pre-manipulation (evening) body mass ($F_{1,35} = 1.501$, $p = 0.312$). However, the overnight decrease in body mass during the night of treatment was greater in wind-exposed than in control groups ($F_{1,35} = 8.019$, $p = 0.008$; figure 1).

(b) Foraging behaviour

Birds in the wind-exposed group used joining to a higher degree than birds in the control group (wind-exposed: 0.69 ± 0.05 , control: 0.34 ± 0.05 ; $F_{1,34} = 13.288$, $p = 0.001$, figure 2). Joining attempt proportion was also higher in the wind-exposed group than in the control group (wind-exposed: 0.15 ± 0.03 , control: 0.12 ± 0.04 ; 'glm' with binomial error distribution: $F_{1,34} = 10.102$, $p = 0.001$). Tactic use was unrelated to pre-manipulation fighting success, indicating that we successfully removed the effects of dominance by selecting middle-ranked individuals (ANOVA, fighting success included as covariate: $F_{1,33} = 0.012$, $p = 0.915$). The treatment did not affect either the overall food intake (number of all pecks by an individual, wind-exposed: 69.05 ± 9.21 , control: 69.65 ± 8.38 ; $F_{1,35} = 0.002$, $p = 0.963$) or the feeding rate of birds (number of pecks per time spent on the grid in seconds, wind-exposed: 0.35 ± 0.04 , control: 0.38 ± 0.03 ; $F_{1,35} = 0.382$, $p = 0.541$). Treatment groups also did not differ in the average number of patches found (wind-exposed: 6.35 ± 0.69 , control: 6.75 ± 0.81 ; $F_{1,35} = 0.152$, $p = 0.699$).

There were no differences between the control and treatment groups either in arrival time on the grid (time in seconds, wind-exposed: 21.80 ± 4.67 , control: 24.90 ± 5.05 ;

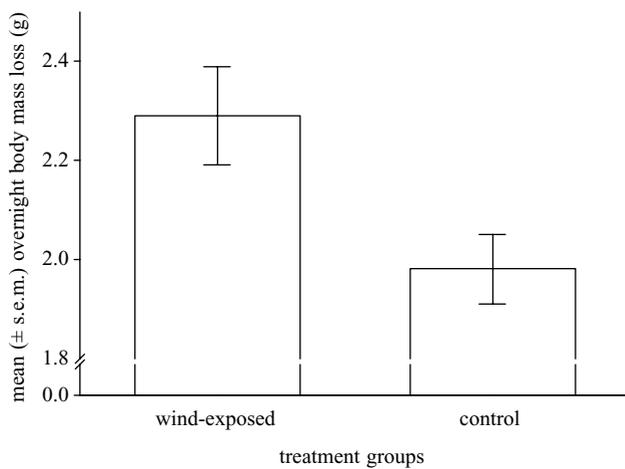


Figure 1. Overnight body mass loss of house sparrows in the wind-exposed and control groups ($n = 20$ individuals in both groups).

$F_{1,35} = 0.216, p = 0.645$) or in the time spent foraging on the grid (time in seconds, wind-exposed: 183 ± 16 , control: 181 ± 13 ; $F_{1,35} = 0.010, p = 0.921$).

(c) Variability and success of foraging strategies

Within-individual variability of patch feeding rates (pecks/s) differed between foraging tactics, with joining having a smaller variance than finding (joining: 0.11 ± 0.02 , finding: 0.15 ± 0.02 ; $F_{1,24} = 5.073, p = 0.034$, figure 3a). The variability of patch finding time was also smaller for joining than for finding (joining: $4.01 + \text{s.e.m. } 1.00, - \text{s.e.m. } 0.83$, finding: $6.35 + \text{s.e.m. } 1.10, - \text{s.e.m. } 0.96$; $F_{1,23} = 4.429, p = 0.046$, figure 3b). On the other hand, there was no significant difference between joining and finding, either in average patch feeding rate (pecks/s; joining: $0.32 + \text{s.e.m. } 0.04, - \text{s.e.m. } 0.03$, finding: $0.30 + \text{s.e.m. } 0.03; - \text{s.e.m. } 0.02$; $F_{1,33} = 0.372, p = 0.546$) or average patch finding time (joining: $7.24 + \text{s.e.m. } 0.97, - \text{s.e.m. } 0.86$, finding: $8.31 + \text{s.e.m. } 0.86, - \text{s.e.m. } 0.78$; $F_{1,33} = 1.198, p = 0.282$).

4. DISCUSSION

In this study we experimentally investigated how the level of energy reserves influences the individual's choice of alternative social foraging tactics. We found that birds exposed to overnight wind responded strongly: they almost doubled the use of joining during their first feeding of the day compared with control birds. This suggests that individuals with lowered energy reserves scrounge more in the morning. Hence, this result provides strong support for the idea that internal state variables (such as energy reserves) play a significant role in decision making about alternative tactic use, not only in solitary individuals (see, for example Thomas 2002a,b; Thomas & Cuthill 2002) but in a social context too. These results underline the importance of the risk of starvation in the animals' foraging decisions. We also showed that variability in both patch feeding rates and patch finding time was smaller for patches discovered by joining than by finding, which supports the idea that scrounging is a risk-averse foraging option compared with producing. Altogether, these findings are in accordance with both an assumption and a major prediction of the

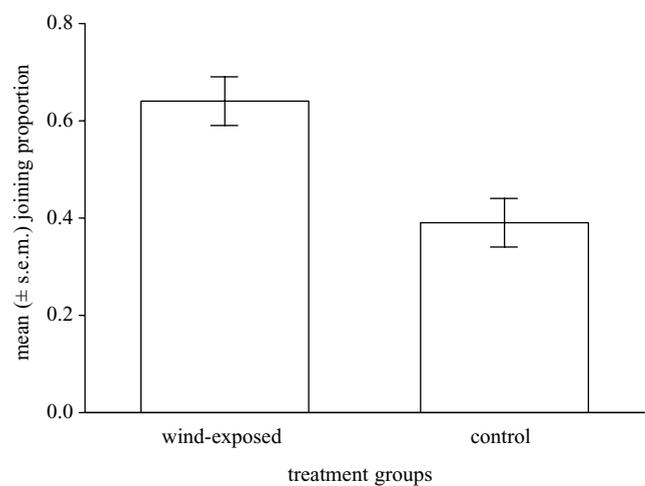


Figure 2. The effect of treatment on foraging tactic use as expressed by the proportion of joining events (for definition of joining, see text). There were 19 individuals in the wind-exposed group and 20 in the control group.

state-dependent dynamic game model presented by Barta & Giraldeau (2000).

The effect of energy reserves on social foraging tactic use has been investigated in small laboratory flocks of European starlings (*Sturnus vulgaris*; Koops & Giraldeau 1996) and nutmeg mannikins (*Lonchura punctulata*; Wu & Giraldeau 2004). By reducing the birds' food intake before the experiments, these investigators found small (non-significant) effects of food deprivation on the use of joining (starlings responded with a small increase whereas mannikins used joining less). These small effects might be explained by the fact that the birds were allowed to accommodate to food deprivation. Thus, birds expecting a shorter foraging period might pre-emptively feed more before the tests, i.e. their reserves might not change as much as could be expected by the length of food deprivation periods.

Despite the significant differences we detected between the foraging tactics in variability of both patch feeding rate and search time, we found no difference in the average success of the tactics as measured by average patch feeding rate and average patch finding time. As joining provided a similar reward to finding, the two experimental groups did not differ in the overall feeding rate and food intake, even though birds in the wind-exposed group used joining to a much greater extent than control birds. This pattern indicates that by using scrounging, sparrows with low energy reserves may reduce the variance of their food intake without considerably diminishing their energy intake.

If the two alternatives provide similar rewards and scrounging may reduce intake variance, then the use of scrounging would usually be profitable for all group members. Note, however, that the payoff of scrounging is negatively frequency-dependent (i.e. as the frequency of scrounging increases in the group, its payoff decreases relative to the payoff of producing; Barnard & Sibly 1981), which prevents the very frequent use of scrounging. As minimizing intake variance may be crucial only for birds with low energy reserves, birds with higher reserves may be 'constrained' to use producing (phenotype-limited games; Parker 1982). It is also noteworthy that house sparrows

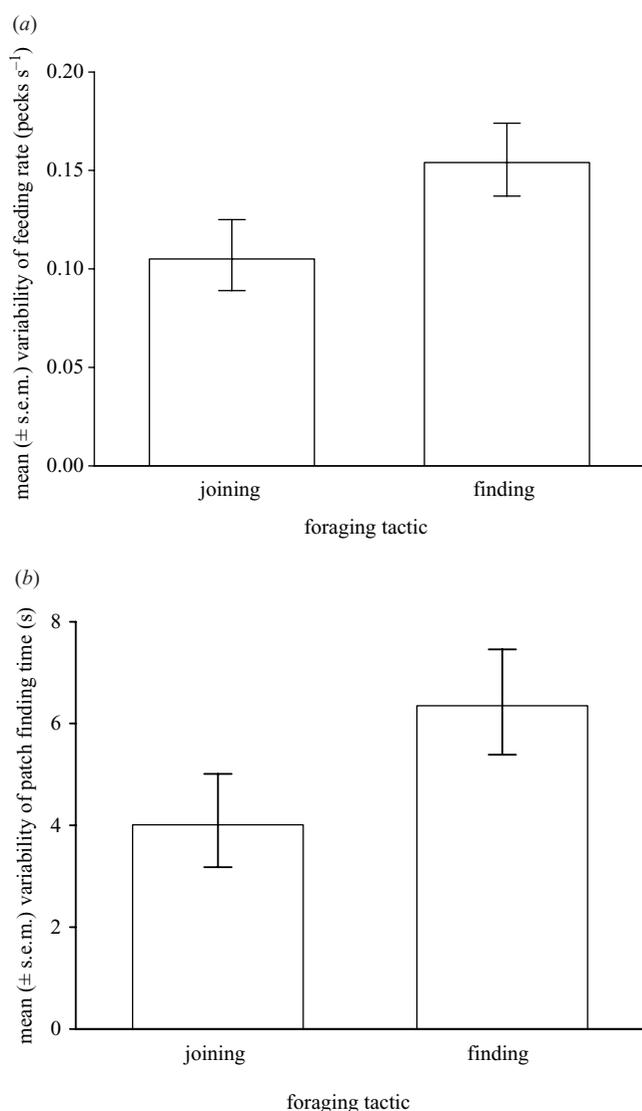


Figure 3. Within-individual variability of (a) patch feeding rates (pecks/s) and (b) patch finding times (s) for different foraging tactics. Variability was measured as the absolute difference from within-individual averages.

often fight aggressively for food patches (finding events were always without aggression, whereas in 44% of joining events birds seized the food patch aggressively); thus scrounging may imply a cost of injury (Liker & Barta 2002). Birds whose energy reserves are far from the critical level can avoid such costs by playing producer. It is still unclear what keeps this producer–scrounger game at equilibrium. Our results clearly show that energy considerations must play a crucial role, but the fact that sparrows frequently fight for food indicates that the costs of aggression may also be important. Future studies, in which both energy reserves and dominance are carefully controlled, should clarify this issue further.

We obtained the present results in flocks where only a few individuals suffered relatively large reductions in their energy reserves. It is at present unclear whether variance reduction in food intake by scrounging also occurs in flocks where the energy reserves of most or all individuals are heavily reduced overnight, e.g. as may be the case in winter flocks of small birds. Variation in morning energy reserves

may be considerable in wild birds (e.g. Broggi *et al.* 2003), because flock members may differ both in their evening energy reserves (i.e. in their starting point before nights) and also in the quality of their roosting sites, which influence the rate of energy loss. Our results apply to middle-ranked birds; thus the effects of energy reserves on tactic use among high- and low-ranked birds remain unknown.

Because in social foraging situations each individual's payoff depends on their companions' behaviour (Maynard Smith 1982; Giraldeau & Caraco 2000), natural selection should favour individuals that are able to respond quickly to changes in their flock mates' behaviour by adjusting their own behaviour. To accomplish this efficiently, individuals are expected to monitor the behaviour of others in the flock. For example, in common cranes (*Grus grus*), where individuals often exploit their flock mates' food discoveries, aggressors increase their vigilance behaviour before attacking a flock mate and hence probably monitor the feeding success of their neighbours. As a consequence, these birds usurp the food resources of those flock mates whose intake rate is higher than average, thereby achieving an immediate increase in their own feeding rate (Bautista *et al.* 1998). Birds might use cues other than flock mates' behaviour, i.e. monitoring the level of energy reserves of others might be a useful predictor of their social behaviour even before foraging. For example, in birds, body mass is known to affect flight performance (Witter *et al.* 1994), thus individuals may use this information to assess the energetic state of their companions.

To summarize, our study provides the first robust empirical evidence that energy reserves may play a significant role in the choice between alternative social foraging tactics. In dominance-based social systems, we recommend further studies to investigate the mutual effects of energy reserves and dominance.

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REFERENCES

- Bakken, G. S. & Lee, K. F. 1992 Effects of wind and illumination on behavior and metabolic-rate of American goldfinches (*Carduelis tristis*). *Auk* **109**, 119–125.
- Barnard, C. J. & Sibly, R. M. 1981 Producers and scroungers: a general model and its application to captive flocks of house sparrows *Anim. Behav.* **29**, 543–550.
- Barta, Z. & Giraldeau, L.-A. 2000 Daily patterns of optimal producer and scrounger use under predation hazard: a state-dependent dynamic game analysis. *Am. Nat.* **155**, 570–582.
- Barta, Z., Liker, A. & Mónus, F. 2004 The effects of predation risk on the use of social foraging tactics. *Anim. Behav.* **67**, 301–308.
- Bautista, L. M., Alonso, J. C. & Alonso, J. A. 1998 Foraging site displacement in common crane flocks. *Anim. Behav.* **56**, 1237–1243.

- Broggi, J., Koivula, K., Lahti, K. & Orell, M. 2003 Seasonality in daily body mass variation in a hoarding boreal passerine. *Oecologia* **137**, 627–633.
- Caraco, T. & Giraldeau, L.-A. 1991 Social foraging: producing and scrounging in a stochastic environment. *J. Theor. Biol.* **153**, 559–583.
- Coolen, I., Giraldeau, L.-A. & Lavoie, M. 2001 Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Anim. Behav.* **61**, 895–903.
- Cuthill, I. C. & Houston, A. I. 1997 Managing time and energy. In *Behavioural ecology*, 4th edn (ed. J. R. Krebs & N. B. Davies), pp. 97–120. Oxford: Blackwell Scientific.
- Cuthill, I. C., Maddocks, S. A., Weall, C. V. & Jones, E. K. M. 2000 Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. *Behav. Ecol.* **11**, 189–195.
- Giraldeau, L.-A. & Caraco, T. 2000 *Social foraging theory*. Princeton University Press.
- Giraldeau, L.-A., Soos, C. & Beauchamp, G. 1994 A test of the producer-scrounger foraging game in captive flocks of spine finches, *Lonchura punctulata*. *Behav. Ecol. Sociobiol.* **34**, 251–256.
- Gross, M. A. 1996 Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **9**, 358–360.
- Herrera, C. M. 1990 Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub. *Oikos* **58**, 277–288.
- Houston, A. I. & McNamara, J. M. 1987 Singing to attract a mate—a stochastic dynamic game. *J. Theor. Biol.* **129**, 57–68.
- Houston, A. I. & McNamara, J. M. 1988 Fighting for food: a dynamic version of the hawk–dove game. *Evol. Ecol.* **2**, 51–64.
- Houston, A. I. & McNamara, J. M. 1999 *Models of adaptive behaviour: an approach based on state*. Cambridge University Press.
- Houston, A., Schmid-Hempel, P. & Kacelnik, A. 1988 Foraging strategy, worker mortality and the growth of the colony in social insects. *Am. Nat.* **131**, 107–114.
- Johnson, C. A., Giraldeau, L.-A. & Grant, J. W. A. 2001 The effect of handling time on interference among house sparrows foraging at different seed densities. *Behaviour* **138**, 597–614.
- Koops, M. A. & Giraldeau, L.-A. 1996 Producer–scrounger foraging games in starlings: a test of mean-maximizing and risk-minimizing foraging models. *Anim. Behav.* **51**, 773–783.
- Liker, A. & Barta, Z. 2001 Male badge size predicts dominance against females in house sparrows. *Condor* **103**, 151–157.
- Liker, A. & Barta, Z. 2002 The effects of dominance on social foraging tactic use in house sparrows. *Behaviour* **139**, 1061–1076.
- Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.
- Mottley, K. & Giraldeau, L.-A. 2000 Experimental evidence that group foragers can converge on predicted producer–scrounger equilibria. *Anim. Behav.* **60**, 341–350.
- Parker, G. A. 1982 Phenotype-limited evolutionary stable strategies. In *Current problems in sociobiology* (ed. King's College Sociobiology Group), pp. 173–201. Cambridge University Press.
- Pinheiro, J. C. & Bates, D. M. 2000 *Mixed-effects models in S and S-Plus*. Berlin: Springer.
- R Development Core Team 2003 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. See <http://www.R-project.org>.
- Steele, W. K. & Hockey, P. A. R. 1995 Factors influencing rate and success of intraspecific kleptoparasitism among kelp gulls (*Larus dominicanus*). *Auk* **112**, 847–859.
- Stephens, D. W. 1981 The logic of risk-sensitive foraging preferences. *Anim. Behav.* **29**, 628–629.
- Stephens, D. W. & Krebs, J. R. 1986 *Foraging theory*. Princeton, New Jersey: Princeton University Press.
- Thomas, R. J. 2002a Seasonal changes in the nocturnal singing routines of common nightingales *Luscinia megarhynchos*. *Ibis* **144**, 105–112.
- Thomas, R. J. 2002b The costs of singing in nightingales. *Anim. Behav.* **63**, 959–966.
- Thomas, R. J. & Cuthill, I. C. 2002 Body mass regulation and the daily singing routines of European robins. *Anim. Behav.* **63**, 285–295.
- Witter, M. S., Cuthill, I. C. & Bonser, R. H. C. 1994 Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Anim. Behav.* **48**, 201–222.
- Wolf, B. O. & Walsberg, G. E. 1996 Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology* **77**, 2228–2236.
- Wu, G.-M. & Giraldeau, L.-A. 2004 Risky decisions: a test of risk sensitivity in socially foraging flocks of *Lonchura punctulata*. *Behav. Ecol.* (In the press.)
- Zerba, E., Dana, A. N. & Lucia, M. A. 1999 The influence of wind and locomotor activity on surface temperature and energy expenditure of the eastern house finch (*Carpodacus mexicanus*) during cold stress. *Physiol. Biochem. Zool.* **72**, 265–276.