



The effects of predation risk on the use of social foraging tactics

ZOLTÁN BARTA*, ANDRÁS LIKER† & FERENC MÓNUS*

*Behavioural Ecology Research Group, Department of Evolutionary Zoology,
University of Debrecen

†Behavioural Biology Research Group, Department of Ecology, Faculty of Veterinary Science,
Szent István University, Hungary

(Received 5 February 2003; initial acceptance 18 March 2003;
final acceptance 23 June 2003; MS. number: 7617)

The effects of predation on the use of social foraging tactics, such as producing and scrounging, are poorly known in animals. On the one hand, recent theoretical models predict increased use of scrounging with increasing predation risk, when scroungers seeking feeding opportunities also have a higher chance of detecting predators. On the other hand, there may be no relation between tactic use and predation when antipredator vigilance is not compatible with scanning flockmates. We investigated experimentally the effects of predation risk on social foraging tactic use in tree sparrows, *Passer montanus*. We manipulated predation risk in the field by changing the distance between shelter and a feeder. Birds visited the feeder in smaller flocks, spent less time on it and were somewhat more vigilant far from shelter than close to it. Increased predation risk strongly affected the social foraging tactic used: birds used the scrounger tactic 30% more often far from cover than close to it. Between-flock variability in scrounging frequency was not related to the average vigilance level of the flock members, and within-flock variability in the use of scrounging was negatively related to the vigilance of birds. Our results suggest that in tree sparrows, the increased frequency of scrounging during high predation risk cannot simply be explained by an additional advantage of increasing antipredator vigilance. We propose alternative mechanisms (e.g. increased stochasticity in food supply, and that riskier places are used by individuals with lower reserves) that may explain increased scrounging when animals forage under high predation risk.

© 2004 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Predation is among the most important factors that influence the foraging behaviour of animals (Lima & Dill 1990). For example, several state-dependent dynamic programming models have shown how the predation–starvation trade-off reshapes the foraging behaviour of solitary birds (e.g. McNamara et al. 1994; Houston & McNamara 1999). For instance, McNamara et al. (1994) found that birds respond to increasing predation risk by decreasing their energetic reserves and their foraging activity throughout the day, except late afternoon. Empirical studies support some of the predictions of these models (e.g. Gentle & Gosler 2001). The effects of predation, however, are less well understood for socially foraging animals, especially with regard to their use of different foraging tactics. In ground-feeding passerines, for

instance, it is common for some of the group members, the producers, to look actively for food, while others, the scroungers, look for individuals that have found food (e.g. Barnard & Sibly 1981; Giraldeau et al. 1990, 1994; Liker & Barta 2002). If scroungers discover a food-finding individual, they join it to feed from its food patch. How is the use of these tactics influenced by predation?

Scroungers, by definition, scan the environment more than producers do. Therefore, the effects of increasing predation risk may be different for the two foraging tactics if scanning for producers also increases the chance of discovering an approaching predator (i.e. the two behaviours are compatible). Consequently, increasing predation risk may increase the use of the scrounger tactic because this may reduce the birds' risk of being preyed upon (Ranta et al. 1998; Beauchamp 2001; Coolen & Giraldeau 2003). Surprisingly, a state-dependent dynamic producing–scrounging game model shows that predation risk affects the frequency of tactic use only if the increase in risk is different for the two tactics, that is, the producers' risk increases faster than the scroungers' risk

Correspondence: Z. Barta, Department of Evolutionary Zoology, University of Debrecen, Debrecen H-4010, Hungary (email: zbarta@delfin.unideb.hu). A. Liker is now at the Department of Zoology, University of Veszprém, H-8201 Veszprém, Hungary.

(Barta & Giraldeau 2000). The dynamic game model also shows that the use of the scrounger tactic will not change with increasing predation risk when the two tactics experience the same predation risk, as would be the case when vigilance and scrounging are incompatible. This lack of effect remains even when other aspects of foraging behaviour, for example, optimal routine, or trajectories of mass, are changed.

The few empirical studies of the effects of predation risk on social foraging have produced conflicting results. Coolen et al. (2001) and Coolen & Giraldeau (2003) have pointed out that nutmeg mannikins, *Lonchura punctulata*, may use different types of behaviour for scanning for food finders and for predators. The mannikins use 'head up while moving' to search for food finders and 'head up while stationary' to detect approaching predators. Consequently, when the perceived predation risk was experimentally increased by increasing the distance between foraging site and protective cover in a laboratory investigation, only the frequency of 'head up while stationary' increased, a response that was not associated with increased frequency of joining flockmates (Coolen & Giraldeau 2003). These results suggest that the two forms of scanning are incompatible in nutmeg mannikins and also support the predictions of Barta & Giraldeau's (2000) model, that is, the frequency of the scrounger tactic does not change with varying predation risk if these behaviours are incompatible. Robinette & Ha (2001) found almost the opposite in a field study of northwestern crows, *Corvus caurinus*: the more time crows spent scanning during a trial, the more likely they were to join another's food discovery, suggesting that use of the scrounger tactic and antipredatory vigilance are compatible. However, Robinette & Ha (2001) did not differentiate between different types of scanning, did not manipulate predation risk, and did not report how predation risk influenced the use of the scrounger tactic. In a recent, semiexperimental study conducted in a game park, Bugnyar & Kotschal (2002) found that free-ranging ravens, *Corvus corax*, used the scrounging tactic more frequently under high risk of predation (obtaining food from a wolf's enclosure) than under low predation risk (foraging from a wild boar's enclosure). In the latter study, in accordance with Barta & Giraldeau's (2000) prediction, predation risk changed disproportionately for the two foraging tactics: producers that entered the enclosure suffered more than scroungers that kleptoparasitized producers outside the enclosure under the more risky condition because wolves aggressively defended their food and even killed scavenging ravens (producers), whereas wild boars did not.

In the present study we experimentally investigated the effects of increased predation risk on social foraging tactic use. It is widely accepted that perceived predation risk increases with distance to cover (Lazarus & Symonds 1992; Pöysä 1994; Lima et al. 1999). Therefore, we increased (as revealed by our tests) the perceived predation risk by increasing the distance between the feeding site and protective cover at a feeding station used by a free-living population of European tree sparrows, *Passer montanus*. Tree sparrows seem to be ideal subjects for investigating the effects of predation on social foraging

because they usually forage in flocks in open places where they are often attacked by predators (Z. Barta, personal observation). Furthermore, the use of both producing and scrounging to find food patches has been shown in their close relative, the house sparrow, *Passer domesticus* (Barnard & Sibly 1981; Liker & Barta 2002). Our approach offers some advantages over the previous studies. First, we experimentally manipulated predation risk. Second, we worked in the field where attacks by predators are common, and where food is unpredictable, not only during treatments but also during the whole day. Consequently, we predicted stronger effects of the manipulation of perceived predation risk than those found in laboratory studies. We also describe some of the behavioural correlates (e.g. landing distance from flockmates, patch-finding rate, etc.) of using the scrounger tactic, which have not been studied in the field for any animal.

METHODS

Study Site and Species

We conducted the study in the Botanical Garden of the University of Debrecen, Debrecen, northeast Hungary. The Garden is mainly an open, bushy area of 0.12 km², containing some buildings and diverse, dispersed patches of coniferous and deciduous trees, and one of its sides is bordered by a forest of about 12 km². Sparrowhawks, *Accipiter nisus*, goshawks, *Accipiter gentilis*, and common buzzards, *Buteo buteo*, are regular visitors in the Garden. We also regularly observed sparrowhawks attacking foraging sparrow flocks and on at least one occasion the attack resulted in the capture of a sparrow. Feral cats are also present. The study was carried out in February 1999, when unusually thick snow covered the area.

The tree sparrow is a small granivorous bird and is one of the most common birds in rural parts of Hungary (Magyar et al. 1998). Six to 10 pairs of tree sparrows breed in the Garden, but in the winter approximately 200–300 individuals regularly forage there (Z. Barta & F. Mónus, personal observation). During the winter, tree sparrows are highly gregarious (Summers-Smith 1995) and groups of 20–30 birds (range 1–70) are common in the Garden (F. Mónus, personal observation). They usually forage in compact flocks in grassy open parts of the Garden but also readily use feeding stations. By the start of the study, 107 tree sparrows were individually colour ringed in this population.

Experimental Procedure

In November 1998 we established a feeding platform on the ground in an undisturbed bushy clearing of the Garden which is regularly used by the sparrows. The platform was made of a plywood sheet (150×150 cm) and it contained 144 holes (2.6 cm in diameter and 1.9 cm deep) arranged in a 12×12 grid where the centres of holes were 10 cm from each other. From the installation of the platform until the beginning of the experiment, corn grit was regularly provided on the platform to familiarize tree sparrows with feeding there. During this period the platform was placed so that its edge was 1.5 m from the closest

bush. As the weather became colder, the sparrows readily used the platform to feed, and used the closest bush as shelter.

The experimental protocol was as follows. We divided the first half of the day (0800–1200 hours) into three stages (i.e. observation periods). At the beginning of each stage the experimenters (Z.B. and F.M.) removed the food from the platform and then placed one teaspoon of corn grit into each of 10 randomly chosen holes. The experimenters then shifted the platform according to a randomly selected treatment (see below) and started a video camera to record the whole surface of the platform for 45 min. The camera was fixed on a tripod 1.5 m above ground and 2 m from the platform. This set-up was a compromise between observing the whole platform and still being able to record vigilance behaviour (see below). When the experimenters moved the platform, the camera was also shifted, so that it was always in the same position relative to the platform. The experimenters then left the platform and returned after 45 min of recording, when the first stage was finished. The second stage was then initialized and the experimenters left the area again and returned 45 min later to initialize the third stage. After the third stage on each day, we deposited some corn grit on the platform.

To manipulate the perceived predation risk, the experimenters placed the platform either near the shelter (the edges of the bush and of the platform were 0.5 m apart; low predation risk) or far from the shelter (the edges were 2.0 m apart; high predation risk). The distance for the far condition was a compromise to get enough birds to forage on the platform, because sparrows were unwilling to forage further away from the bush (Z. Barta, personal observation). Treatments were randomly ordered for the three stages within a given day, fulfilling the constraint that both treatments must have occurred at least once a day. To check whether individual sparrows use the platform in only one of the treatment positions, the experimenters recorded the presence of as many colour-ringed individuals as possible on the platform. These recordings were done during the video recordings from a remote location by binoculars. However, the behaviour of these colour-ringed individuals was not analysed as they could not be identified on the tapes. Sparrow flocks spent some time in the bush next to the platform before visiting the platform to feed. To forage, they sequentially landed on the platform, building up groups of up to about 50 individuals. The flocks typically left the platform suddenly, en masse.

Manipulations were carried out on 2, 4, 9–13 and 15–17 February 1999. As the procedure during the first 3 days (i.e. on 2, 4 and 9 February) served to habituate the sparrows to the food distribution and our activity, videotapes recorded during these days were not included in the subsequent analyses. In total, 945 min of tapes were analysed from 10 and 11 observation periods at close and far distances from the shelter, respectively.

Data Analysis

We analysed the video recordings as follows. First, we defined a trial as each occasion when at least one sparrow

stayed on the platform ($N = 480$). Then we recorded the length of trials (from the landing of the first sparrow until the departure of the last one), and coded the maximum number of arriving sparrows as 1, 2, ..., 5, 5+. For each trial we also recorded whether another species (commonly Eurasian blackbirds, *Turdus merula*, and great tits, *Parus major*) fed with the sparrows. Second, we analysed randomly chosen trials in detail from those 202 trials where more than five sparrows were present and no other species used the platform at the same time. Since the detailed analysis of sparrows' behaviour (see below) was time consuming and we had limited access to the video-analysing equipment, we could analyse only 114 trials in this way. These trials were digitized and analysed frame-by-frame. For each digitized trial, we recorded the maximum number of sparrows observed on the platform as a surrogate of group size, the length of the trial (in these analyses a trial ended when fewer than five sparrows remained on the platform), and the coordinates (according to the grid of holes, see above) of the vertex of the smallest convex polygon fitted on the flock just before the end of the trial. From these coordinates we then calculated the area occupied by the flock which we used to calculate the density of birds.

In each of the 114 trials, we randomly chose three individuals from the flock and recorded their behaviour in detail. To describe foraging methods of sparrows, we divided feeding events into two types, finding and joining. We use these terms instead of producing and scrounging, respectively, because we recorded actual feeding events and not directly observed tactic use, that is, whether a bird was searching as a producer or as a scrounger (Mottley & Giraldeau 2000; Coolen et al. 2001). We defined a feeding event as joining when the hole from which the focal bird fed was occupied by another feeding bird immediately before or at the moment of the arrival of the focal individual. A hole was obtained by finding if it was unoccupied when found by the focal individual (no other bird within 10 cm of the hole when the focal bird arrived within 10 cm; Liker & Barta 2002). We considered the sampled bird's head to be in a head-up position if the line from the joint of the upper and lower mandibles to the tip of the bill was at or above the horizontal. The distance and the angle from which we recorded the birds did not always allow precise observation of bill position; nevertheless, in these cases the white cheek patch and the white neck collar of tree sparrows made it possible to categorize head position correctly.

From the videotapes, the following variables were measured for each sampled individual in each trial. We defined joining and finding frequency as the number of holes found by joining and finding, respectively. The proportion of joining, that is, the frequency of joining divided by the total number of holes used for feeding by the sampled bird during the trial, was then used as a surrogate of foraging tactic use. The number of pecks from found and joined holes was also recorded. Scanning rate was defined as the number of frames on which the sampled bird's head was in the head-up position divided by the number of frames on which the bird was

continuously present on the platform. For arriving birds we also recorded the bird's distance from its nearest flockmate (distances according to the grid of holes). The coordinates of birds at arrival and departure (according to the grid of holes), the time spent from arrival until the discovery of the first patch, and whether the first patch was produced or scrounged were also recorded. To characterize flocks, we averaged these variables within flocks in some analyses (e.g. average use of joining, see below).

Statistical Analyses

All analyses were done by the **R** statistical computing environment (Ihaka & Gentleman 1996). Data were mainly analysed by fitting linear and generalized linear models (GLMs, Crawley 1993). Entering the confounding variables in these types of analyses can be interpreted as statistically removing (controlling for) the effects of these variables.

Data were analysed at two levels. First, the effects of treatment on perceived predation risk and foraging behaviour were studied at the level of trials, that is, using trials as independent data points. In these cases, we averaged behavioural data within the trial (i.e. average of the three randomly chosen individuals). For variables describing trials (e.g. group size, total time spent on the platform by the flock), or behaviour of an average group member (e.g. average time spent on the platform, average proportion of time spent vigilant, average use of joining) we entered the days and the order of stages as confounding variables. We explicitly state when we controlled for other variables in some analyses (e.g. when we removed the effects of flock size).

Second, we analysed behavioural variation within groups (i.e. within trials) at the level of individuals (see *Within-group correlates of joining*). In these analyses, we investigated whether within-group variability in the use of foraging tactics was associated with within-group variability in other aspects of the birds' behaviour, for example, level of vigilance or foraging success. In these analyses, we entered trials as a confounding variable (this also removed the effects of days, stages and treatments).

To handle non-normal distribution in data we used GLMs (glm function of **R**; Venables & Ripley 1999) with appropriate error distributions and link functions: gamma error with logarithmic link for, for example, exponentially distributed time variables, and binomial error with logit link for binomially distributed patch-finding events (Venables & Ripley 1999). The appropriate test statistic for these models is χ^2_1 (Venables & Ripley 1999). Otherwise, we used linear models (lm function of **R**; Venables & Ripley 1999), with the usual *F* statistics. Means \pm SD of untransformed data and two-tailed probabilities are given throughout.

We are aware that some of our data may be pseudoreplicated, that is, some of the observed individuals could be the same. To estimate the degree of this pseudoreplication we carried out a Monte Carlo 'experiment' to mimic our sampling procedure. In this 'experiment' we randomly and independently sampled three birds 114

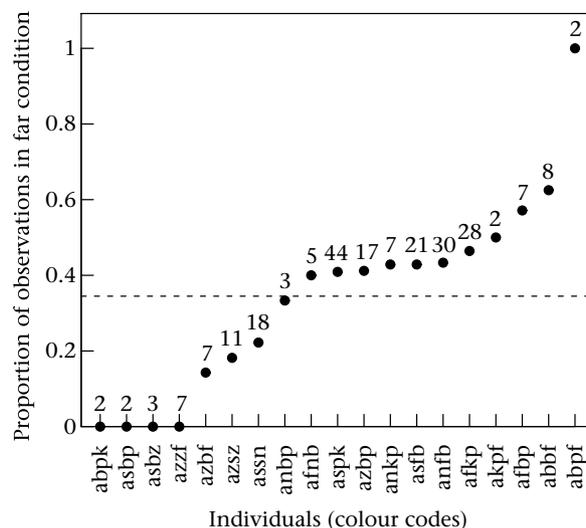


Figure 1. Proportion of observations in the far condition (feeding platform far from shelter) for each individually identified sparrow seen at least twice on the platform during the stages of the experiment. The dashed line indicates the mean proportion averaged across individuals. Numbers above the points show the number of observations for each individual.

times out of 200 birds (the lower, more conservative estimate of the winter population size of sparrows in the Garden), where the sampling distribution (the probability that a given bird is sampled) was derived from the observation frequency of colour-ringed birds (Fig. 1). We then counted the number of different individuals in these 114 by three samples. This procedure was carried out 1000 times and shows that on average 104.7 ± 4.36 birds were independently sampled. According to this 'experiment', our conclusions are based on the observations of a large number of different individuals which makes it unlikely that our results are biased by a few oddly behaving birds.

RESULTS

Perceived Predation Risk

We observed 33 ringed individuals on the platform, 238 times in total. Of the 238 occasions, we observed them 151 times (63.4%) in the near condition, which indicates that the sparrows preferentially used the platform when it was close to the shelter. For the 19 sparrows we saw at least twice, we investigated their platform usage under the different treatments (Fig. 1). Individuals on average foraged less on the platform in the far condition (34.5%; one-sample Wilcoxon test on average individual proportions: H_0 : mean, $\mu = 0.5$; $V = 28$, $N = 19$, $P = 0.013$).

The preliminary analyses of the tapes also showed that sparrows differed in their behaviour between treatments. Of the 480 groups (group size ≥ 1) we observed during the video recording (including those not analysed in detail), 22.4 groups/stage used the platform in the far condition and 23.4 groups/stage used it in the near one. Groups consisted of five or more individuals in 79.1% of cases in the near condition and this decreased to 69.1% of cases

in the far condition ($\chi_1^2 = 5.66$, $P = 0.017$). Groups spent significantly less time on the platform in the far condition (15.62 ± 14.69 s) than in the near condition (23.98 ± 21.54 s; GLM, $\chi_1^2 = 19.144$, $P < 0.001$).

For the 114 trials analysed in detail, the maximum group size was somewhat higher in the near condition (24.4 ± 10.14 versus 19.9 ± 11.65) but the difference was not significant between treatments ($F_{1,104} = 0.313$, $P = 0.577$; however, we analysed trials only where flocks were larger than five individuals, see [Methods](#)). The time spent by the flocks on the platform increased with maximum group size ($\chi_1^2 = 3.982$, $P = 0.046$), and differed significantly between treatments (far condition: 14.6 ± 11.47 s; near condition: 21.3 ± 15.74 s; gamma error with logarithmic link, after controlling for group size: $\chi_1^2 = 7.977$, $P = 0.005$). The average time spent on the platform by an individual also increased with maximum group size ($\chi_1^2 = 13.485$, $P < 0.001$), and it was shorter under the far condition (9.6 ± 8.96 s; near condition: 12.1 ± 8.99 s) but not significantly so (gamma error with logarithmic link, after controlling for maximum group size: $\chi_1^2 = 2.607$, $P = 0.106$).

In both treatments, sparrows arrived close to the edge of the platform that was nearest to the shelter ('near edge'). They landed close to the near edge independently of group size when the platform was far from the bush ([Fig. 2](#)), but when the platform was close to the shelter the landing sparrows' distance from the near edge increased with group size (treatment versus group size interaction: $F_{1,102} = 4.395$, $P = 0.039$; [Fig. 2](#)). Nevertheless, the density of the departing sparrows was higher in the near condition (gamma error with logarithmic link: $\chi_1^2 = 3.955$, $P = 0.047$).

Average vigilance rate decreased significantly with increasing group size ($F_{1,104} = 15.955$, $P < 0.001$). Birds also tended to spend a slightly higher proportion of time scanning in the far condition (0.50 ± 0.153) than in the near condition (0.44 ± 0.153 ; after removing the effects of group size: $F_{1,103} = 3.512$, $P = 0.064$).

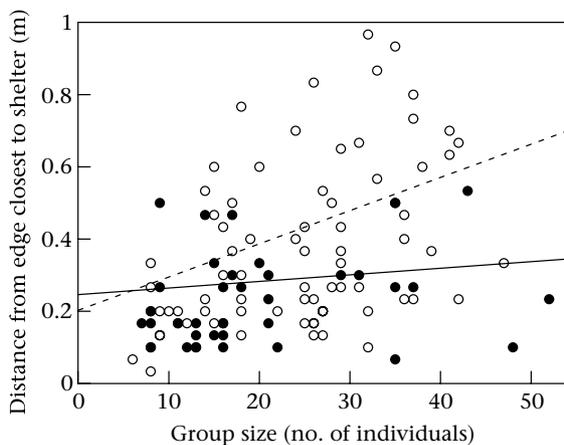


Figure 2. Distance of landing sparrows from the edge of the feeding platform closest to a bushy shelter. ○: Platform near bush; ●: platform far from bush. Lines are the regression lines between group size and distance after effects of days and stages were removed (---: near condition; —: far condition).

Effect of Treatment on Foraging

Of the 342 occasions we observed the foraging behaviour of sparrows, they did not find any patches 21 times. On those occasions (321) when the sparrows found at least one patch they mostly used the finding tactic exclusively (54.8%) but they sometimes (9%) used only joining ([Fig. 3](#)). On the remaining occasions (36.1%) they alternated between tactics. An average individual obtained $21.81 \pm 31.16\%$ of its patches by joining.

The average use of joining in a group did not correlate with the average vigilance ($\chi_1^2 = 0.865$, $P = 0.352$) and it increased with group size ($\chi_1^2 = 5.874$, $P = 0.015$). Furthermore, individuals joined more when far from shelter (mean proportion of patches found by joining = 0.28 ± 0.217) than when near it (0.18 ± 0.186 ; after removing the effect of group size: $\chi_1^2 = 11.326$, $P < 0.001$; [Fig. 4](#)). The group size by treatment interaction was not significant ($\chi_1^2 = 0.181$, $P = 0.671$).

The average patch-finding rate, defined as the average number of patches found by an individual divided by the average time spent on the platform, did not differ between treatments (far condition: 0.39 ± 0.221 patches/s; near condition: 0.35 ± 0.135 patches/s; $F_{1,104} = 0.49$, $P = 0.486$). Average pecking rate also did not differ between treatments (far condition: 1.37 ± 0.388 pecks/s; near condition: 1.44 ± 0.373 pecks/s; $F_{1,104} = 0.558$, $P = 0.457$).

Within-group Correlates of Joining

Within-group joining decreased strongly as within-group vigilance increased ($\chi_1^2 = 8.947$, $P = 0.003$; [Fig. 5](#)). The distance between the landing individual and its nearest neighbour also influenced the rate of within-group joining; the closer the individual landed to another individual, the more it joined ($\chi_1^2 = 10.812$, $P = 0.001$; [Fig. 6](#)). This effect cannot be accounted for by our definition of feeding events (i.e. finding can happen only if no other birds are present within 10 cm), because the sparrows frequently moved on the platform (on average 33.8 cm between the points of arrival and departure), so a sparrow

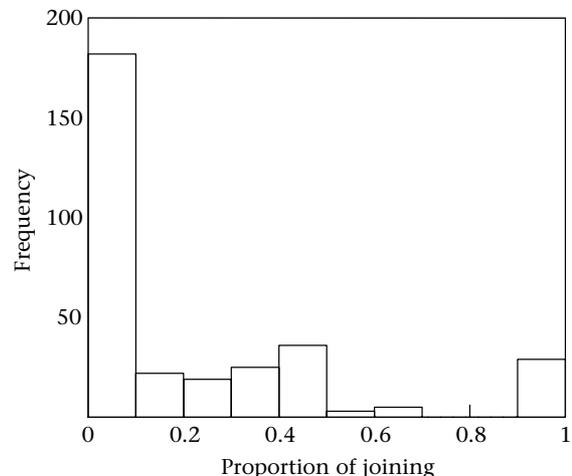


Figure 3. Distribution of the proportion of joining feeding flockmates for all sampled individuals foraging on a feeding platform.

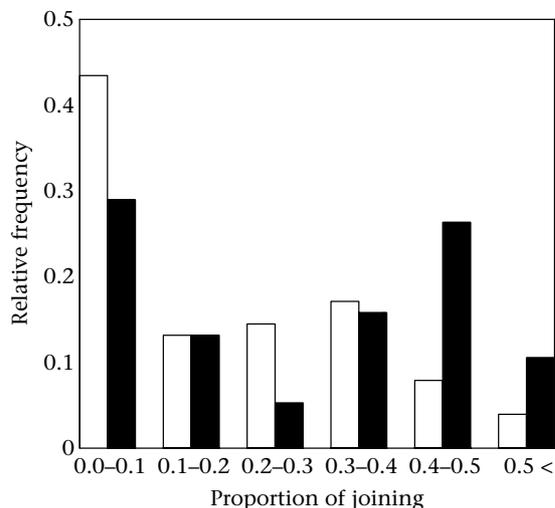


Figure 4. Distribution of the proportion of joining feeding flockmates (averaged within trials) when the feeding platform was near a shelter (□) or far from it (■).

that arrived close to another bird could move away and find patches alone. The time an individual spent on the platform until the discovery of its first patch did not depend on whether this patch was produced or scrounged ($F_{1,120} = 0.022$, $P = 0.881$, on log-transformed time). The proportion of joining correlated negatively with the number of patches (including both produced and scrounged ones) from which the individuals fed per unit time ($\chi^2_1 = 5.428$, $P = 0.02$) and positively with pecking rate ($\chi^2_1 = 7.546$, $P = 0.006$). Thus, the individuals that used joining more frequently fed from fewer patches but consumed more food from a given patch.

DISCUSSION

In this study, our first aim was to explore whether joining is used in a free-living population of birds. We found that flock-feeding tree sparrows frequently used both searching

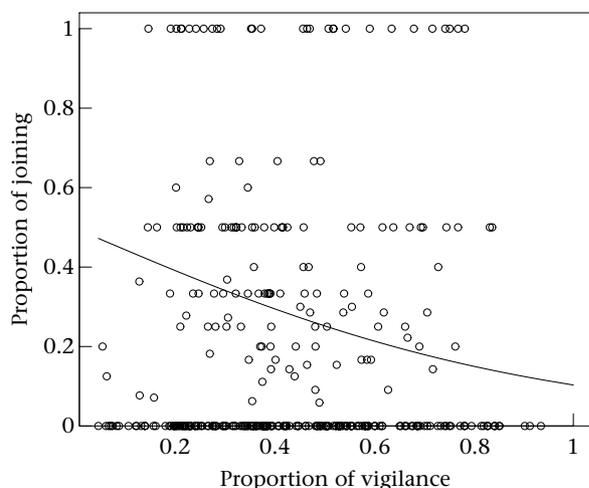


Figure 5. Effect of within-group vigilance rate on the proportion of joining feeding flockmates. The line is fitted by a generalized linear model (GLM) function (see text).

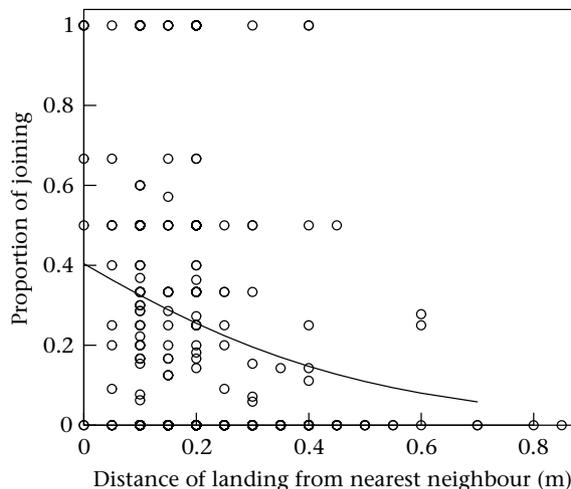


Figure 6. Effect of distance of landing from the nearest neighbour on subsequent joining of feeding flockmates. The line is fitted by a generalized linear model (GLM) function (see text).

and joining to find food in our study set-up. The average frequency of joining (22%) was broadly similar to that we found in a laboratory study of house sparrows (17%, Liker & Barta 2002), thus may be typical for sparrows feeding on rich and clumped food patches. The foraging tactic use of tree sparrows seems to be flexible in the sense that 36% of the birds were observed to use a mixture of both tactics, as has also been found in house sparrows (Barnard & Sibly 1981; Liker & Barta 2002).

Our second aim was to investigate whether a change in predation risk affects social foraging tactic use, as predicted by some recent producer–scrounger models (e.g. Ranta et al. 1998). To our knowledge, this is the first experimental test of the problem conducted in the field with free-ranging animals. We found that altering predation risk affected the relative frequency of joining: birds joined significantly more frequently when they foraged far from cover than when they foraged close to it (about 30% more joining in the far condition).

At first sight, this result seems to support the model developed by Ranta et al. (1998). They assumed that antipredator vigilance is compatible with scanning for joining opportunities. Therefore, increasing predation risk may increase the birds' use of joining because this may reduce their risk of being preyed upon. Thus, based on Ranta et al. (1998), one can predict a positive correlation between antipredator vigilance (including scanning for joining opportunities) and joining frequency (Beauchamp 2001). The analysis of birds' behaviour on a finer scale, however, reveals that we obtained almost the opposite results. Although scanning rate was slightly higher far from shelter than close to it, we found no correlation between scanning rate and joining frequency when we analysed the relation at the level of groups. Furthermore, when we investigated within-group variability, a strong negative correlation was found between scanning rate and joining frequency. These results do not support the assumption that scrounging and vigilance are compatible activities (Ranta et al. 1998). Instead, the pattern we observed between vigilance and joining is similar to the patterns

reported by Coolen et al. (2001) and Coolen & Giraldeau (2003), and suggests that there may be different behavioural adaptations for antipredator vigilance and for monitoring joining opportunities in free-living tree sparrows.

If more frequent joining was not the result of increased vigilance, then why did joining increase with increased predation risk in our experiment? Recent theoretical work (Caraco & Giraldeau 1991; Barta & Giraldeau 1998, 2000) suggests several factors that may lead to increased use of joining. First, both Caraco & Giraldeau (1991) and Barta & Giraldeau (2000) showed that scrounging is a risk-averse foraging tactic compared to producing: scrounging individuals have a higher chance of obtaining food patches than producers do. Our treatment reduced the time available to feed during a period of high predation risk by 30% which might have resulted in higher stochasticity in food supply. Thus, if joining represents a risk-averse tactic in sparrows, individuals might have preferentially used it in the far condition to reduce the stochasticity in their food supply. Second, Barta & Giraldeau's (2000) model predicts that individuals with low reserves should use the scrounger tactic more frequently than birds with high reserves, especially early in the day. Consequently, if the relative frequency of birds with low reserves increases under high predation risk (i.e. because they cannot afford to wait until conditions become safer; Houston et al. 1993), one would predict more scrounging there. Based on our data we cannot exclude this explanation. Our colour-ringed birds did not show a strong preference to forage on the platform only under one treatment but we did not know the body condition of birds using the platform under different predation risks. Third, Barta & Giraldeau (1998) predicted that the proportion of scrounging would increase as the extent of competitive differences between individuals decreases. If increasing predation risk decreases the benefits of resource defence (e.g. because individuals cannot afford time for it), then the competitive asymmetries between individuals may decrease, which in turn may lead to an increased frequency of joining. Since our experiment was conducted in the field where conditions are much harsher than in the laboratory, one would predict that any of those factors could have a strong effect. This could explain why Coolen & Giraldeau (2003) could not find an effect of increasing predation risk on foraging tactic use in a laboratory study while we could.

The finding that the birds fed at lower density far from the shelter indicates that our result cannot be attributed to more birds finding the same patches by chance alone when the density is high. We found that rate of joining correlated positively with group size as predicted by several producing–scrounging models (e.g. Caraco & Giraldeau 1991; Vickery et al. 1991). This result (with the strong negative correlation between group size and vigilance) indicates that our measure of group size and vigilance was a realistic surrogate of the true group size and vigilance. As indicated by the correlation between the nearest-neighbour distance of landing individuals and their subsequent use of joining, the sparrows seemed to decide which tactic to use before landing on the platform. One may, however, argue that this is simply the

consequence of birds leaving the shelter only when they can join another bird on the platform, that is, when they have just observed an individual find food. As the time needed to discover the first patch after arriving did not depend on whether the patch was found or joined, this argument seems to be unjustified.

In conclusion, our study showed that tree sparrows responded to increasing predation risk by increasing the use of the joining tactic during social foraging. Our results suggest, however, that an increase in antipredator vigilance does not explain the increase in joining rate, and that antipredator scanning may even be costly in terms of reduced detection of joining opportunities. Further studies are needed to investigate which of the proposed mechanisms is responsible for the change in tactic use.

Acknowledgments

We are grateful to I. Coolen, L.-A. Giraldeau and two anonymous referees for their valuable comments on the manuscript. We thank J. Serfőző and J. Szentpéteri for their assistance in the field work, and K. Pecsénye for allowing access to her video digitalizing equipment. M. Szabó and the staff of the Garden kindly helped our work there. Z.B. and A.L. were supported both by a Bolyai János Research Fellowship and a Békesy György Postdoctoral Fellowship. During the preparation of the manuscript Z.B. held a Marie Curie Research Fellowship. The study was supported by OTKA grants T030434 to Z.B. and F026595 to A.L.

References

- Barnard, C. J. & Sibly, R. M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour*, **29**, 543–550.
- Barta, Z. & Giraldeau, L.-A. 1998. The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing–scrounging game. *Behavioral Ecology and Sociobiology*, **42**, 217–223.
- Barta, Z. & Giraldeau, L.-A. 2000. Daily patterns of optimal producer and scrounger use under predation hazard: a state-dependent dynamic game analysis. *American Naturalist*, **155**, 570–582.
- Beauchamp, G. 2001. Should vigilance always decrease with group size? *Behavioral Ecology and Sociobiology*, **51**, 47–52.
- Bugnyar, T. & Kotschal, K. 2002. Scrounging tactics in free-ranging ravens, *Corvus corax*. *Ethology*, **108**, 993–1009.
- Caraco, T. & Giraldeau, L.-A. 1991. Social foraging: producing and scrounging in a stochastic environment. *Journal of Theoretical Biology*, **153**, 559–583.
- Coolen, I. & Giraldeau, L.-A. 2003. Incompatibility between antipredatory vigilance and scrounger tactic in nutmeg mannikins, *Lonchura punctulata*. *Animal Behaviour*, **66**, 657–664.
- Coolen, I., Giraldeau, L.-A. & Lavoie, M. 2001. Head position as an indicator of producer and scrounger tactics in a ground feeding bird. *Animal Behaviour*, **61**, 895–903.
- Crawley, M. J. 1993. *GLIM for Ecologists*. Oxford: Blackwell Scientific.
- Gentle, L. K. & Gosler, A. G. 2001. Fat reserves and perceived predation risk in the great tit, *Parus major*. *Proceedings of the Royal Society of London, Series B*, **268**, 487–491.

- Giraldeau, L.-A., Hogan, J. A. & Clinchy, M. J. 1990. The payoffs to producing and scrounging: what happens when patches are divisible. *Ethology*, **85**, 132–146.
- Giraldeau, L.-A., Soos, C. & Beauchamp, G. 1994. A test of the producer–scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata*. *Behavioral Ecology and Sociobiology*, **34**, 251–256.
- Houston, A. I. & McNamara, J. M. 1999. *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.
- Houston, A. I., McNamara, J. M. & Hutchinson, J. M. C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London, Series B*, **341**, 375–397.
- Ihaka, R. & Gentleman, R. 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.
- Lazarus, J. & Symonds, M. 1992. Contrasting effects of protective and obstructive cover on avian vigilance. *Animal Behaviour*, **43**, 519–521.
- Liker, A. & Barta, Z. 2002. The effects of dominance on social foraging tactic use in house sparrows. *Behaviour*, **139**, 1061–1076.
- Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- Lima, S. L., Zollner, P. A. & Bednekoff, P. A. 1999. Predation, scramble competition, and the vigilance group size effect in the dark-eyed juncos (*Junco hyemalis*). *Behavioral Ecology and Sociobiology*, **46**, 110–116.
- McNamara, J. M., Houston, A. I. & Lima, S. L. 1994. Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology*, **25**, 287–302.
- Magyar, G., Hadarics, T., Waliczky, Z., Schmidt, A., Nagy, T. & Bankovics, A. 1998. *Nomenclator Avium Hungariae*. Budapest—Szeged: Madártani Intézet—BirdLife Hungary—Winter Fair [in Hungarian].
- Mottley, K. & Giraldeau, L.-A. 2000. Experimental evidence that group foragers can converge on predicted producer–scrounger equilibria. *Animal Behaviour*, **60**, 341–350.
- Pöysä, H. 1994. Group foraging, distance to cover and vigilance in the teal *Anas crecca*. *Animal Behaviour*, **48**, 921–928.
- Ranta, E., Peuhkuri, N., Hirvonen, H. & Barnard, C. J. 1998. Producers, scroungers and the price of a free meal. *Animal Behaviour*, **55**, 737–744.
- Robinette, R. L. & Ha, J. C. 2001. Social and ecological factors influencing vigilance by northwestern crows, *Corvus caurinus*. *Animal Behaviour*, **62**, 447–452.
- Summers-Smith, J. D. 1995. *The Tree Sparrow*. Guisborough: Privately published.
- Venables, W. N. & Ripley, B. D. 1999. *Modern Applied Statistics with S-PLUS*. 3rd edn. New York: Springer.
- Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L. & Chapman, C. A. 1991. Producers, scroungers, and group foraging. *American Naturalist*, **137**, 847–863.