Ethology

The Effect of Within-Flock Spatial Position on the Use of Social Foraging Tactics in Free-Living Tree Sparrows

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Received: July 19, 2007
Initial acceptance: August 28, 2007
Final acceptance: October 17, 2007
(G. Beckers)

doi: 10.1111/j.1439-0310.2007.01472.x

Abstract

The benefit of producer (searches for own food) or scrounger (exploits the others' food discoveries) foraging tactic in a group of socially feeding animals may depend on where the individual searches for food within the group. Scrounging may be more advantageous in the centre of the group, having more individuals around to join, while producing may be more beneficial at the edges, where more unexplored food patches may be found. This study shows within-flock position correlates with foraging tactic use of feeding birds in socially foraging tree sparrows, *Passer montanus*. Sparrows staying closer to the centre of the flock found their food patches more frequently by joining (i.e. use more frequently the scrounging tactic) than those staying toward the edges. To our knowledge this is the first field study demonstrating the relationship between spatial position and foraging tactic use. We investigated this relationship under different perceived predation hazard, and found that under elevated risk of predation, central individuals may increase their use of joining more than individuals on the periphery of the flock. Moreover, we show that extremely specialized use of searching tactics may be very infrequent in tree sparrows. As both within-flock position and search tactic use can be altered very quickly and without leaving the flock, individuals may easily alter them in order to adjust their behaviour.

Introduction

Foraging in groups often leads to the appearance of individuals (the scroungers) who do not search directly for food, but search for joining opportunities to exploit others' (the producers') food discoveries (Brockmann & Barnard 1979; Barnard & Sibly 1981; Barnard 1984). During foraging it is assumed that an individual may choose to follow either the producer or the scrounger tactic, and can switch freely between these at any moment (Giraldeau & Caraco 2000; Coolen et al. 2001; Coolen & Giraldeau 2003; Fernández-Juricic et al. 2004). The search tactic chosen can depend on internal factors, such as energy reserves or condition (Koops & Giraldeau 1996; Barta & Giraldeau 2000; Lendvai et al. 2004), and on external factors, such as the distribution of food (Caraco & Giraldeau 1991), ambient temperature (Caraco et al. 1990), competitive ability of flockmates (Barta & Giraldeau 1998; Liker & Barta 2002; Lendvai et al. 2006), or predation pressure (Barta et al. 2004).

A rarely investigated external factor that may affect the use of search tactics is the spatial position within the flock. A spatially explicit model (Barta et al. 1997) predicts that individuals in the centre of the flock can detect more opportunities to join and can quickly approach an individual having found a food patch. Thus, it may be more beneficial to scrounge for individuals in the centre compared with those on the periphery of the flock. On the other hand, individuals may have a better chance to find unexploited food patches on the periphery of the flock, i.e. producing may be more advantageous on the periphery.

To investigate the relationship between the use of search tactics and spatial position, Flynn & Giraldeau (2001) performed an experiment on nutmeg manikins (*Lonchura punctulata*) using hidden food patches. Prior to the experiment they trained a portion of experimental birds to find the hidden food patches allowing them to choose freely between producer and scrounger tactics, while untrained ones were constrained to scrounge. Birds constrained to feed only by scrounging occupied positions closer to the centre of the flock than trained ones as predicted by the model. To our knowledge, however, no study on free ranging animals has investigated the role of within-flock spatial position on the use of social foraging tactics. Neither we have any knowledge on whether other important aspects of foraging, e.g. predation risk, may alter the effect of within-flock position on social foraging tactic use.

Here we investigate how the use of social foraging tactics correlates with spatial position within the flocks in free-living European tree sparrows (*Passer montanus*) under different predation hazards. Tree sparrows seem to be the ideal subjects for investigating the effect of within-flock position on social foraging because they usually forage in flocks in open places where the observation of the entire flock can be easily carried out. Furthermore, the use of the producer and the scrounger food searching tactics has been previously shown in this species (Barta et al. 2004). We video-recorded tree sparrows feeding in flocks under different predation hazards, and we used these records to determine the within-flock spatial positions of the individuals and the foraging tactics they employed to acquire food patches. In order to analyse behavioural traits close to each other in time, we recorded the within-flock spatial position of the birds just before their departure from the feeding platform and investigated how this position correlates the way by which the focal bird obtained its previous food patch.

Methods

Study Site and Species

This study was conducted on tree sparrows (*P. montanus*) in the Botanical Garden of the University of Debrecen, Debrecen, Hungary, in the winter of 1999. For a detailed description of the study site see Barta et al. (2004). In winter, when tree sparrows are highly gregarious (Summers-Smith 1995) approximately 200–300 individuals regularly foraged in the garden in groups of various sizes (range 1–70; Zoltán Barta and Ferenc Mónus, personal observations). They usually foraged in grassy open parts of the garden but also readily used feeding stations. By the start of the study, 107 tree sparrows were individually colour-ringed in this population.

Experimental Procedure

This study is based on the same video-recordings as that of Barta et al. (2004). Detailed description of the experimental procedure is published there; therefore in this section we restrict our description only to some crucial details.

Videotapes of 945 min from 7 d between 10 and 17 February 1999 were analysed (on 14 February no video-recordings were taken). Tapes were recorded after familiarization of sparrows at a feeding platform. The size of the platform was 150 by 150 cm and it contained 144 holes (2.6 cm in diameter and 1.9 cm deep). The holes were arranged in a 12 by 12 grid, and their centres were 10 cm from each other. During the experiment we supplied small amounts of corn grit at the bottom of a few randomly chosen holes inducing sparrows to search actively on the entire surface of the platform. During recordings the camera was mounted on a tripod which was placed at a fixed position relative to the platform (1.5 m above ground and 2 m from the platform). This camera view allowed us to observe the entire surface of the platform, but prevented the identification of colour codes of ringed birds. This was a compromise taken in order to ensure the correct recording of the within-flock spatial position of individuals. Parallel to the video-recordings, birds feeding on the platform were simultaneously observed from a remote location using binoculars, and we identified as many colour-ringed individuals as possible. Although the behaviour of the identified birds could not have been analysed, their observation frequency was used to run a Monte Carlo simulation. This simulation aimed to estimate the degree of multiple observations of the same unidentified birds (see Statistical Analyses).

Video-recordings were carried out in the mornings (0800–1200). Each morning was divided into three stages, i.e. three periods of recording of 45 min. Before each stage we placed the platform either near to the shelter (a bush) or far from it to alter perceived predation risk of the sparrows. The feeding platform was perceived more hazardous by sparrows when the edge of the platform was placed 2.0 m from the bush (far condition) than when it was placed at 0.5 m from the bush (near condition). Results supporting the effectiveness of the manipulation are published in Barta et al. (2004). Before each stage, we removed all food from the platform, randomly chose 10 holes to present food (one teaspoon of corn grit per hole) then started the video camera to record. Then we left the platform and returned after 45 min of recording to initiate the next stage. After the third stage we deposited a greater amount of corn grit on the platform, so that the birds could forage there in the whole afternoon.

Sparrows initiated foraging bouts from the bush nearest to the platform. Flock members landed sequentially, quickly following each other. Birds typically left the platform suddenly en masse, i.e. usually all birds departed simultaneously.

Data Collection

We recorded 480 foraging trials when at least one sparrow stayed on the platform. Out of these we analysed the same randomly chosen 114 trials as in Barta et al. (2004). In each of these trials at least six sparrows were present and no other species used the platform at the same time. The end of these trials was defined when fewer than six sparrows remained on the platform. For these trials we recorded the area occupied by the flock and the maximum number of sparrows observed on the platform as a surrogate of group size. During the trials analysed in detail the maximum number of sparrows ranged from 6 to 52 with a median of 21.5. The majority of the birds participating in a given foraging trial arrived to the platform in a few seconds and they usually stayed there throughout the foraging bout, i.e. the maximum number of sparrows was approached soon during the trial (Zoltán Barta and Ferenc Mónus, personal observations). The area occupied was calculated from the coordinates of individuals at the vertices of the smallest convex polygon fitted on the flock just before the flushing of the individuals (coordinates were recorded according to the grid of holes). We calculated the density of birds as the maximum number of sparrows observed during the trial divided by the area they used for foraging.

The detailed behaviour of three randomly chosen birds per trial was recorded. Variables characterizing within-flock spatial position were recorded just before the focal individual left the platform. In 98% of the observations (335 out of the 342 cases) the focal bird left the platform with the flush of the flock, which took 0.38 ± 0.31 s in average ($n = 114$). In such cases, position variables were recorded just before the departure of the first flockmate rather than that of the focal bird. To characterize within-flock position we used two measures: the distance of the focal individual to the centre of the flock and centrality. Distance to the centre was calculated as the distance between the departing individual and the centre of gravity of the smallest convex polygon fitted on the flock before the flushing of the individuals (both expressed as coordinates according to the grid of the holes). Centrality was a binary measure; we categorized the focal bird as feeding on the 'edge' or in the 'middle' of the flock based on whether it stayed on the outline of the smallest convex polygon fitted on the flock or did not.

To assess the use of scrounging tactic we categorized feeding events into two types: finding and joining. We defined finding and joining events as in Barta et al. (2004). The hole from which the focal bird fed was considered to be obtained by joining when it 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 used the finding and joining terms as surrogates for producing and scrounging, respectively, because we recorded actual feeding events and not directly observed whether a bird is searching using the producer or the scrounger tactic (Mottley & Giraldeau 2000; Coolen et al. 2001). To explore the relationship between joining and within-flock positions we analysed only the last feeding event of the individuals. This was the closest event in time to the moment when their within-flock position was recorded. As sparrows find a food patch nearly in every 3 s in average (Barta et al. 2004), the last patch-finding event of an individual and the time when its position was recorded must be as close as within a few seconds in most cases. Note also that this procedure could be considered as a random sampling in respect to the foraging processes on the platform because the birds left simultaneously and their departures occurred mostly as a response to some external events (e.g. alarm calls).

For each focal bird we recorded the arrival coordinates (according to the grid of holes) in order to calculate the linear distance between the point of the arrival and the departure, and the time that the focal individuals spent on the feeding platform. The sparrows did not find any food patch in 21 cases out of the 342 analysed feeding bouts and in some cases missing variables occurred, therefore sample size in our analyses were smaller than 342.

Statistical Analyses

Data were analysed by fitting generalized linear mixed effects models (*lmer* function in R; Bates & Sarkar 2005). Generalized linear models allow to choose different error distributions rather than the normal distribution (Crawley 1993), while mixed effects models allow to define both fixed and random effect variables (Zar 1984). We chose the binomial error distribution and the logit link function to analyse the type of patch-finding events (as in Barta et al. 2004) and entered trials as a random factor in the model. We entered fixed effect variables sequentially. In this type of analysis the effect of a variable entered in the model is analysed as if the effects of all previously entered variables were statistically controlled for. In order to correctly analyse the effect of the within-flock position, we always entered it in the model as the last variable. Using mixed effects models – in this case considering a random variance component derived from the diversity of the trials, which arise from several known (e.g. flock size, days, stages) and unknown (e.g. flock composition, weather, presence of predators) effects – increases the validity of the results and provides a very robust statistical test (Zar 1984). All analyses were carried out in the R interactive statistical environment (R Development Core Team. 2006).

We are aware that our sampling procedure does not exclude pseudoreplication, i.e. some of our observations could be collected from the same individuals. To assess the extent to which this pseudoreplication affects our results we estimated the number of sampled sparrows by the means of a Monte Carlo simulation that was used to imitate our sampling procedure. We randomly and independently sampled three birds 114 times out of 200 birds (the lower, more conservative estimate of the wintering sparrow population in the garden), then we counted the different individuals in the sample. We repeated the sampling procedure 1000 times. The sampling distribution of individuals (the probability that a given bird was sampled) was derived from the observation frequency of colour-ringed birds feeding on the platform during the video-recordings (see Fig. 1 in Barta et al. 2004). This experiment revealed that our conclusions are based on the observations of a large number of different individuals (104.7 ± 4.36 based on a conservative estimation) and it is unlikely that our results are biased by a few oddly behaving birds.

Results

Changes in Position and Tactic Use

Birds readily changed their within-flock position as both focal individuals and their flock-mates moved continuously on the platform when searching for food (Ferenc Mónus, personal observation). The linear distance between the point of the arrival and the departure of the focal birds varied from 0 up to 1.1 m with median 0.3 m (n = 284), but the trajectories of the actual movements were very likely longer. Sparrows used the entire surface of the platform for feeding and spent 0.5–75 s with a median of 8.5 s (n = 342) on it.

The searching tactic used by the sparrows changed also during the trials: 49% of the birds that found at least two patches used both finding and joining to feed. Moreover, as the number of the found food patches increased among these individuals, the proportion of birds that used both finding and joining increased monotonously (number of found patches: 2 [n = 79], 3 [n = 49], 4 [n = 32], 5 [n = 22], more than 5 [n = 55]; and the respective proportions: 32%, 43%, 50%, 64% and 73%; $r_s = 1$, $p < 0.017$, n = 5).

The Effect of Position on the Use of Joining

We analysed whether predation hazard (platform close to or far from the bushy shelter), density of birds or within-flock position affected the type of patch-finding events. Two mixed effects generalized linear models were constructed: first we entered in both models the density of birds and then predation hazard; finally, we entered distance to centre of the flock and its interaction with predation hazard in the first model, and centrality and its interaction with predation hazard in the second model. We found the following results. Density had a significant effect on joining occurrence; sparrows used the joining behaviour more frequently as density increased (first model: $F_{1,307} = 7.361$, $p = 0.006$; second model: $F_{1,307} = 6.501$, $p = 0.011$). Predation hazard also had a significant effect; sparrows find their patches more frequently by joining far from the shelter than near to it (first model: $F_{1,307} = 5.552$, $p = 0.022$; second model: $F_{1,307} = 6.251$, $p = 0.013$). Finally, both distance to

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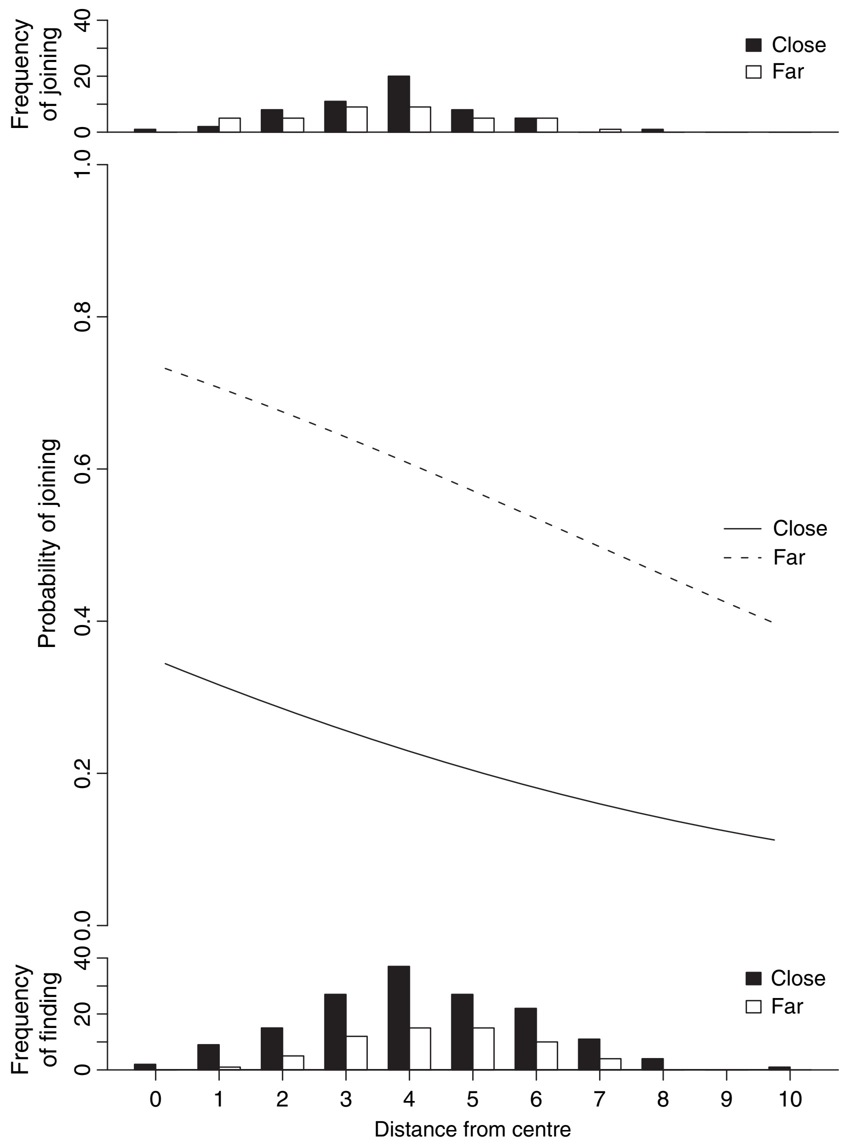

Fig. 1: The bottom and the top panels show the frequency of finding and joining events at a given distance from the centre of the flock under different predation hazard (close to and far from the bushy shelter), respectively. The middle panel shows how the probability of joining changes in relation to the distance from the centre of the flock as predicted by the mixed effects generalized linear model.

the centre of the flock and centrality significantly correlated with the use of the joining behaviour. The farther from the centre a sparrow foraged, the lower was the probability that it found its food patch by joining (Fig. 1; $F_{1,307} = 6.712$, $p = 0.010$); equivalently, the sparrows feeding on the edge of the flock found their patches less frequently by joining than the sparrows in the middle of the flock (Fig. 2; $F_{1,307} = 17.225$, $p < 0.001$). The interaction term of predation hazard by distance to centre of the flock in the first model was not found to be significant ($F_{1,307} = 1.705$, $p = 0.193$). However, the interaction term of predation hazard by centrality in the second model was significant ($F_{1,307} = 5.763$, $p = 0.017$). This reveals that the difference in the use of joining between central and peripheral individuals is more expressed under the far condition; the individuals in the middle of the flock increase their joining frequency under elevated predation hazard, while individuals on the edge do not alter it (Fig. 2). Any other interaction terms were not proved to be significant and were omitted from the final, reported models.

Discussion

Recent theoretical work predicts that group-feeding animals should locate at the periphery of the group if they search for undiscovered food patches, while should occupy central places if they search for

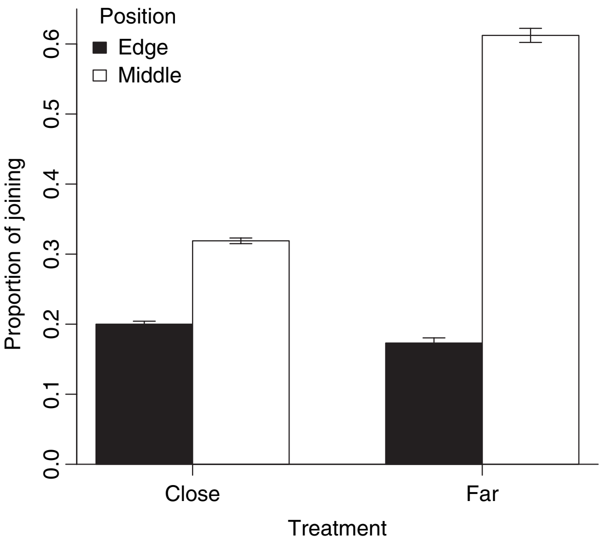

Fig. 2: The mean proportion of food patches (±SE) found by joining by tree sparrows feeding on the edge and in the middle of the flock under different predation hazard (close to and far from the bushy shelter).

opportunities to exploit others' discoveries (Barta et al. 1997). In this study, we investigated the relationship of within-flock spatial position and the use of search tactics on free-ranging individuals of a small passerine, the tree sparrow, *P. montanus*, when feeding on clumped resources delivered on the ground under different predation risks. We found that the proportion of patches found by joining is less when sparrows feed farther from the centre of the flock than close to it and when feed on the edge of the flock compared with ones feeding in the middle. Our results are in accordance to those of a laboratory study on nutmeg manikins, *L. punctulata* (Flynn & Giraldeau 2001), and support the main prediction of the model by Barta et al. (1997), i.e. central positions may be more advantageous to use the scrounging tactic, while on the periphery of the flock finding tactic may be more beneficial. To our knowledge this is the first study demonstrating this relationship on free-living animals.

We previously found that the proportion of joining use increases when birds feed under elevated predation hazards (Barta et al. 2004). In the present study, we analysed only one patch-finding event per focal bird in contrary to the previous work when each patch-finding event was included. Results confirm the previous finding using a very robust statistical test (mixed effects model, see Statistical Analyses). Moreover, comparing the strength of the effect of within-flock position on tactic use under low and high predation risk conditions reveals additional knowledge. In the case of centrality, the change in joining occurrence between birds on the edge and in the middle of the flock was different between treatments. Fig. 2 shows that the increase in joining under high predation risk is mainly attributable to the birds feeding in the middle of the group, while individuals on the edge do not seem to alter the use of joining behaviour. However, we did not find a similar difference between treatments regarding the effect of the distance to the centre of the flock. This inconsistency might be explained by that these two measures can be differently sensitive to the uncontrolled variation in flock shape and within-flock distribution of individuals.

One might argue that the depletion level of food can differ between the two treatments as birds spent more time on the platform when it was near to the shelter (Barta et al. 2004). This fact is likely not to affect our results because birds returned to the platform within a few seconds after departure.

The time point we chose to record spatial position (immediately before departure) may be considered as a random moment during feeding, as before the flushing of the first sparrow supposedly none of the individuals prepares for leaving the feeding platform at the next moment. Therefore, our findings may represent a general rule of feeding behaviour applicable to the most foraging situations. However, Flynn & Giraldeau (2001) mentioned that birds adopted the predicted spatial pattern only after certain latency. In their experiment they did not find difference in the flock geometry during the first two minutes of the feeding bouts between flocks containing high and low frequency of scroungers, but they found during the remainder of the trials. They explained this difference with the different spatial rules that may drive the arrival and the further feeding behaviour of birds. In our study we investigated very short feeding bouts (up to 75 s); the use of joining behaviour was still unmistakably related to the within-flock spatial position of birds. We suppose that under natural conditions birds may adopt optimal spatial patterns very quickly, also during feeding events as short as only few seconds.

We observed that feeding sparrows quickly change both their within-flock position and the searching tactic they actually use. Within-flock position of a bird may change both when a bird itself moves and when its flock-mates move. As a consequence of the continuous movements of the flock members, within-flock position of a bird may change at any moment. On the other hand, searching tactic may also change very quickly; birds may use both searching tactics even when spending only a few seconds on the feeding platform. We found that 49% of the birds having found at least two patches used both finding and joining to feed. Birds must quickly switch between tactics considering that sparrows find a food patch nearly in every 3 s on average (Barta et al. 2004). These observations underline that flocking animals may choose their searching tactic or their within-flock position in order to quickly adjust their behaviour to approach the actually optimal one. Moreover, both tactic use and choice of position may serve as very fine manners allowing behavioural adjustments without leaving the flock or the actual feeding place.

Our correlation-based results regarding the relationship of within-flock position and the use of foraging tactics raise two questions. (1) Whether individuals seeking for joining opportunities occupy central positions while producers aspire towards the periphery or individuals close to the centre simply have more opportunities to join successful flockmates. Based on our data we cannot prove or exclude either of these possibilities, although the study of Flynn & Giraldeau (2001) suggests that birds may actively choose their within-flock position according to the search tactic they use. (2) Whether the spatial pattern of the search tactic use we observed is the result of the differences in pay-offs of tactics when they are used in the centre of the flock or at the periphery (as predicted by the model of Barta et al. 1997) or the results of other mechanisms disregarded in this study. Another possible explanation of our observations may be the effect of dominance hierarchy. Dominants may try to retain central positions safer from predation, while subordinates are forced to forage at the periphery (e.g. Janson 1990). As dominants are expected to use scrounging tactic more often than subordinates (Barta & Giraldeau 1998; Liker & Barta 2002; Lendvai et al. 2006), such spatial differences in the distribution of dominant and subordinate individuals may lead to similar spatial pattern of search tactic use. As tree sparrows often involve in aggressive encounters (Summers-Smith 1995; Zoltán Barta and Ferenc Mónus, personal observations) we cannot exclude the latter explanation. Further studies are needed to investigate whether difference in the payoff of search tactics in central and peripheral positions, spatial distribution of dominants and subordinates or both affects the spatial pattern of search tactic use in species foraging in dominance-structured flocks.

We found moreover that the proportion of birds observed to use both searching tactic rapidly increased from 32% to 73% as we recorded more patch-finding observations of the individual birds. These results suggest that individuals using exclusively one searching tactic must be infrequent; however, under certain circumstances there is obviously a preference of individuals to use one or the other searching tactic (e.g. Liker & Barta 2002; Lendvai et al. 2006; but note these studies investigated house sparrows, a related species).

Finally, the proportion of joining use also correlated positively with the density of birds in the feeding flock. This result is in accordance with our previous finding that proportion of joining correlated positively with the group size (Barta et al. 2004) and both results support the prediction of several producing–scrounging models (e.g. Caraco & Giraldeau 1991; Vickery et al. 1991).

In conclusion, our study shows that the spatial position occupied by individuals within the foraging flock may have a crucial role in determining important aspects of foraging behaviour. Individuals foraging in the middle of the flock may have more possibility to adjust their use of social foraging tactic in the case of an altered feeding situation, e.g. under changing predation risk. However, within-flock position can be altered very quickly and without leaving the flock and may help individuals to approach optimal behaviour under the given conditions.

Acknowledgements

The authors are grateful to J. Serfőző and J. Szentpéteri for their assistance in the fieldwork, and to K. Pecsenye for allowing access to her video digitalizing equipment. M. Szabó and the staff of the garden kindly helped this work. Ferenc Mónus was supported by a PhD scholarship; Zoltán Barta was supported by an Öveges scholarship. The study was supported by OTKA grants NF 61143 and T-46661.

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