

Outline of PhD thesis

SOCIAL FORAGING IN TREE SPARROWS

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I. INTRODUCTION

Behavioural decisions of animals are arranged around two main questions, how to reproduce and how to survive. From the perspective of their genes, it is very important when, how and with whom they reproduce. On the other hand, they have to survive between reproductive seasons; and they have to do it in the best possible condition. From the point of view of the total life span of the individuals, the life history strategies incorporate these two main questions in one lifelong trade-off.

In my PhD thesis, I investigate the behavioural decisions of flock feeding birds made in order to maximize their survival between reproductive seasons. Maximizing the chance of survival generally involves two main issues: proper feeding (appropriate composition, quantity and temporal distribution of food) and avoiding predators, i.e. minimizing the risk of starvation and predation simultaneously. These two factors are supposed to have been the main evolutionary forces leading to in the evolution of group-living and group-foraging (Krause & Ruxton 2002). Group-foraging may be advantageous both against predators (Lima & Dill 1990) and in terms of efficiency or predictability of foraging (Beauchamp 1998). Thus, a shift from solitary to gregarious foraging may be an excellent way to abate the conflict between starvation and predation.

The investigation of group-foraging is essential to understand gregarious behaviour. When trying to understand group-foraging, one has to recognize factors affecting the behaviour of solitary foragers, and additionally, the potential interactions between flockmates. It is frequently observed among group-foragers that some individuals do not actively search for food, but search for opportunities to join or to monopolize other's food discoveries.

Those individuals searching actively for their own food discoveries are called producers, while those joining food patches found by their flockmates are called scroungers (Barnard & Sibley 1981, Barta 2002).

The joining behaviour provides an excellent example how the behaviour of individuals in a group affects the behaviour of flockmates, since the gain from joining depends strongly on how others behave. As the proportion of producers decreases in the group, scroungers do worse because more scroungers share the fewer food patches found by the fewer producers. In contrast, when the proportion of producers increases, scroungers do better and choosing the scrounger tactic becomes more and more beneficial (**Fig. 1**). Consequently, there is a stable equilibrium proportion of scrounging in the group.

The producer-scrounger game (Vickery et al. 1991, Barta 2002) draws the attention to several important questions. For example, why do producers flock together with scroungers instead of leaving them in order to establish flocks without scroungers? Which advantages are conferred by the presence of scroungers to the individuals of the flock? Several studies provide evidence that the producer-scrounger game allows for risk-sensitive decisions (Barta & Giraldeau 2000, Lendvai et al. 2004); therefore even the existence of the possibility to choose the scrounger tactic may be advantageous for the members of the group.

Our knowledge on the producer-scrounger game is based on elaborated theoretical models; however, the supporting empirical evidence, especially field studies are frequently absent. Therefore I aimed to test the predictions of several recent theoretical models in the field. As a study species I chose the tree sparrow (*Passer montanus*). Individuals in the winter flocks of this ground feeding passerine bird frequently use the scrounger tactic; furthermore, this behaviour can be observed easily as tree sparrow

is a common species and tolerates human observers well. During the field studies on the producer-scrounger game, I also encountered and investigated several other phenomena concerning group-foraging (e.g. dominance hierarchy and status signals).

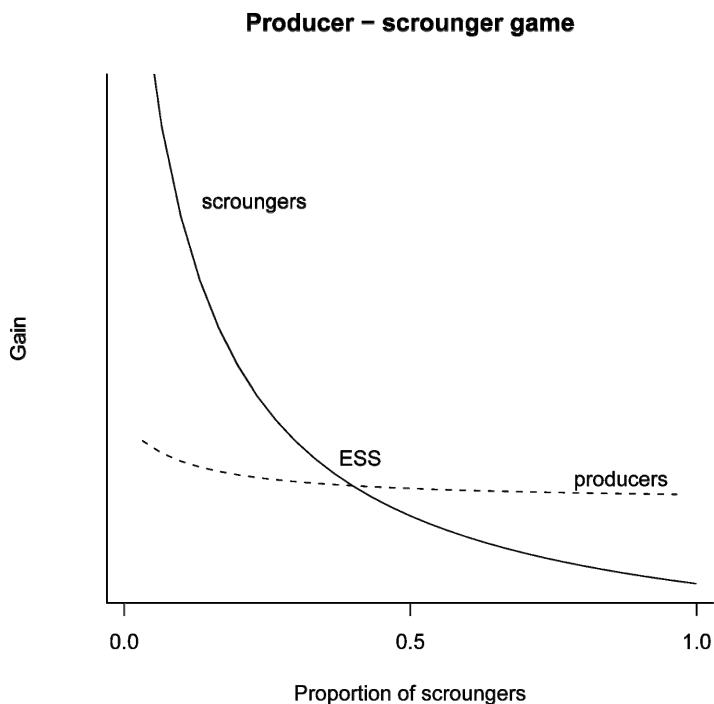


Fig. 1 The gain from scrounging shows strong negative frequency dependency. The gain from producing decreases much more slowly than that of scrounging with the increasing proportion of scroungers. The intersection of the two curves marks the stable equilibrium proportion of the two tactics in the group which is an evolutionary stable strategy (ESS). Based on the work of Vickery et al. (1991).

II. AIMS

- (1) I investigated the effect of perceived predation hazard on the behavioural decisions of group-foraging birds using experimental manipulation.

The effect of predation risk on the foraging activity (*Chapter 4.1.*) was studied, as previous studies reported contradictory results. Some of these studies revealed that small passerine birds decrease their foraging activity or efficiency under high risk of predation in order to avoid being preyed upon (e.g. van der Veen 2000). However, there are other works providing evidence that under certain conditions decreasing foraging activity may carry as high a risk as predation. For instance, during short winter days the risk of not attaining the energy level necessary to survive the following night may be serious (Polo et al. 2007).

I examined the effect of predation risk on the synchronization of movements of individuals (arrivals at and departures from a food patch; *Chapter 4.1.*). Synchronized movements of individuals may be advantageous against predators by confusing them in the selection and the capture of their prey (Humphries & Driver 1967). Nevertheless, to our knowledge, this behaviour has never been investigated in anti-predatory context.

I also studied the effect of predation risk on the use of producer and scrounger social foraging tactics (*Chapter 4.2., 4.3.*). In the case of higher predation risk, it may be beneficial to use the scrounger tactic if scanning for successful producers also increases the chance of discovering an approaching predator (Ranta et al. 1998).

- (2) I investigated whether the use of social foraging tactics correlates with the spatial position of individuals within the flock, as predicted by a spatially explicit producer-scrounger model (Barta et al. 1997; *Chapter 4.3*). According to this model, it is more beneficial to use the scrounger tactic in the middle of the flock, because individuals may be able to detect more opportunities to scrounge and they may join them more quickly. Producing may be more beneficial at the edge of the flock, because there is a higher chance of discovering new food patches at the edges.
- (3) Based on the observations of individually identified birds, I investigated the relationship between fighting success of individuals and their use of different forms of joining behaviour (aggressive and non-aggressive forms; *Chapter 4.4*). Although several studies study the relationship between social foraging tactic use and dominance-rank or fighting success, these works do not usually consider different forms of joining behaviour (but see: Liker & Barta 2002).
- (4) Based on behavioural observations, biometric data and DNA-based sexing of individuals, I examined whether the size of the black bib may signal dominance status to flockmates in tree sparrows; as it is frequently found in bird species with black-coloured feather ornamentation (*Chapter 4.5*). The only study to date investigating the signalling role of the bib in tree sparrows yielded contradictory results (Torda et al. 2004).

III. RESULTS

- (1) Foraging activity and efficiency did not change with the manipulation of the perceived predation risk. Birds were constrained to forage in order to reach the required level of energy reserves, even under high risk of predation. Furthermore, birds continuously and intensively foraged during the daylight hours without lowering their foraging activity during the day, which also supports the previous conclusion. These results support the view that short daylight hours during the winter set a challenging task for small passerines trying to attain the level of energy reserves required by the long and cold nights.

Tree sparrows in a flock landing on the feeder synchronized their arrivals more when the predation hazard is higher (**Fig. 2**). This behaviour may be advantageous against predators; and to my knowledge this is the first study investigating this behaviour.

Tree sparrows used the joining behaviour more frequently when the predation hazard is higher (**Fig. 3**). However, those individuals that joined more frequently showed a lower level of vigilance. Consequently, the increase in joining frequency was not attributable to the compatibility between scanning for flockmates and for predators, but it may supposedly be due to the risk-averse nature of the scrounging foraging tactic.

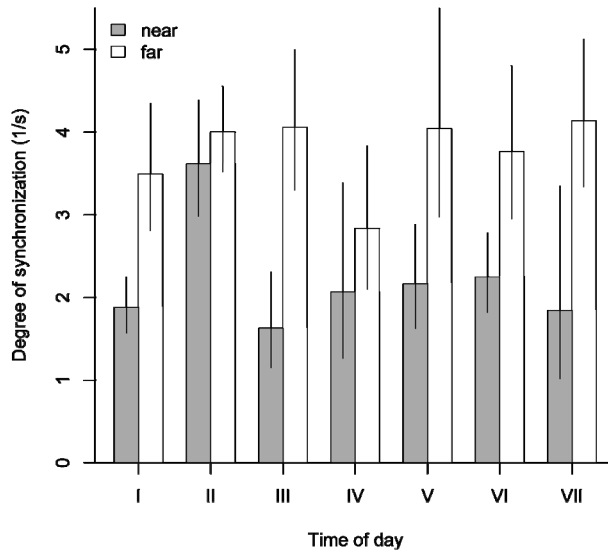


Fig. 2 The degree of synchronization (reciprocal of the time elapsed between arrival of the fifth and the tenth bird) at the arrival to the feeder in winter flocks of tree sparrows near to and far from the shelter in relation to the time of day. Bars show back-transformed values of mean \pm SE of the log-transformed values. (Effect of treatment: $\chi^2_1 = 14.352$, $p < 0.001$; effect of time of day: $\chi^2_6 = 5.812$, $p = 0.445$; $n = 222$; linear mixed effect model)

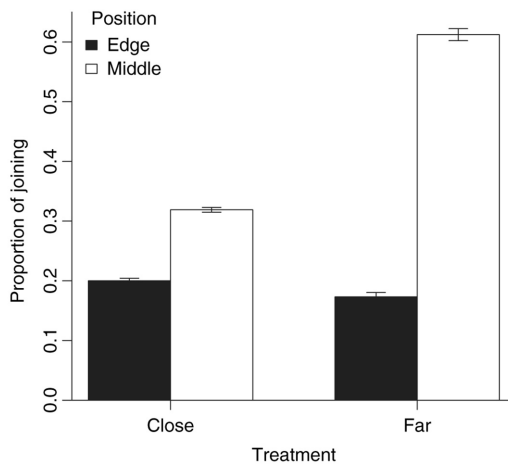


Fig. 3 The mean proportion of food patches (\pm SE) found using joining by the sparrows feeding on the edge and in the middle of the flock under different predation hazard, i.e. close to and far from the bushy shelter. (Effect of treatment: $F_{1,307} = 6.251$, $p = 0.013$; effect of position: $F_{1,307} = 17.225$, $p < 0.001$; interaction: $F_{1,307} = 5.763$, $p = 0.017$; linear mixed effect model)

- (2) Flock members foraging in the middle of the group used the scrounging tactic more frequently than their flockmates at the edge of the group. To my knowledge, this is the first time this was shown in the case of free-living animals. When the risk of predation increases, flock members in the middle of the group are those that may significantly increase the frequency of joining use (**Fig. 3**).
- (3) The proportion of food patches found by joining and the proportion of fights won correlated positively in case of individual tree sparrows, in accordance with other studies. Furthermore, as the fighting success of individuals increased, the frequency of aggressive joining also increased, while the frequency of non-aggressive forms of joining decreased (non-aggressive joining and timid stealing; **Fig. 4**).

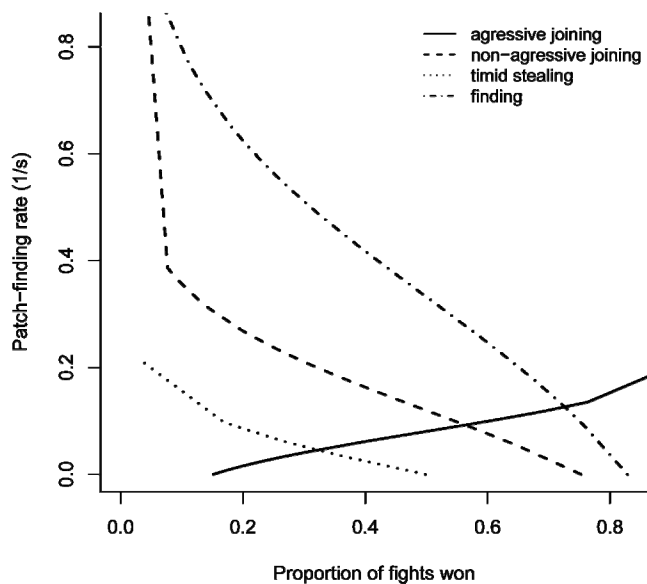


Fig. 4 The rate of patch-finding with different forms of joining and with finding in relation to the proportion of fights won by individual sparrows. Lines represent the predictions of the linear mixed-effect models ($\chi^2_1 > 17.381$, $p < 0.001$; for all cases).

- (4) I found all morphological size measurements greater in males than in females. Behavioural observation of individuals of known sex revealed that a major proportion of the variance of the fighting success of males could be explained by the size of the black bib; individuals with a greater bib had higher fighting success. In females, fighting success did not correlate with the size of the bib; it correlated positively with wing-length, and negatively with tarsus-length. Based on these results, it is possible that in tree sparrows males use the size of the bib as a status signal, while females do not. The variance of bib size was greater in males than in females, while the variance of no other trait differed between the sexes, further supporting the above presumption.

IV. CONCLUSIONS

The results of my PhD thesis confirm the significant role of group-foraging and gregarious behaviour in avoidance of predators. On the other hand, they draw the attention to the importance of investigating group behaviour in addition to individual behaviour. The results concerning the effect of predation hazard on the use of joining behaviour bear new insights how predation hazard may shape the probability of food finding; and through this effect how it may change the social behaviour of individuals. My results show that the within-flock spatial position of individuals is an important factor determining which behavioural option is the most beneficial for an individual. Furthermore, based on their within-flock spatial position, individuals respond differently to changes in the predation risk. Within-flock spatial position may critically affect behavioural decisions as it can be varied quickly and without obvious costs. Consequently, changing spatial position may easily contribute to finding the optimal or a suboptimal behavioural response under the given circumstances without leaving the flock. My results provide evidence that tree sparrows form dominance-structured foraging groups during the winter; and competitive differences of individuals may strongly affect the use of social foraging tactics. My work reveals that tree sparrows flexibly vary the use of producer and scrounger tactics according to the current environmental conditions. Furthermore, exclusive use of one tactic in the case of individuals may be very infrequent.

My results support the hypothesis that the size of the black bib may signal dominance status in tree sparrows. Moreover, they draw attention to the possibility that functions associated with morphological traits may differ between sexes in the case of sexually monomorph species.

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VII. PUBLICATIONS INCLUDED IN THE THESIS

Published papers:

- Mónus, F. & Barta, Z. 2008. The effect of within-flock spatial position on the use of social foraging tactics in free-living tree sparrows. **Ethology**, 114:215-222. IF: 1.99
- Barta, Z., Liker, A. & Mónus, F. 2004. The effects of predation risk on the use of social foraging tactics. **Animal Behaviour**, 67:301-308. IF: 2.09
- Mónus, F. & Barta, Z. 2010. Seasonality and sociality in tree sparrows *Passer montanus*. **International Studies on Sparrows**, *in press*.

Manuscripts:

- Mónus, F. & Barta, Z. Synchronized feeding initiation as an anti-predatory response in Tree Sparrow flocks. (submitted: **Behaviour**)
- Mónus, F., Szabó, K., Lózsza, A., Péntzes, Zs. & Barta, Z. Intersexual size and plumage differences in Tree Sparrows (*Passer montanus*) – a morphological study based on molecular sex determination. (submitted: **Acta Zool. Acad. Sci. H.**)
- Mónus, F. & Barta, Z. Foraging activity of European Tree Sparrows under predation risk. (manuscript in preparation)

International conference abstracts:

- Mónus F., Barta, Z. & Liker, A. Spatial position and social foraging tactic use in European tree sparrows (*Passer montanus*). 9th International Behavioral Ecology Congress, Montreal, Canada 7-12th July 2002.
- Mónus, F., Liker, A. & Barta, Z. The effect of changing predation hazard on the use of scrounger foraging tactic. XXVII International Ethological Conf., Tuebingen, Germany 22-29th Aug. 2001.
- Mónus, F. & Barta, Z.: Individual movements in Tree Sparrow. 15th International Conference of the European Bird Census Council. Nyíregyháza, Hungary 26-31st March 2001.