Degree of synchronization of tree sparrows in flocks under different predation risk

Ferenc Mónus[1] **& Zoltán Barta**

(Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, Egyetem tér 1, H-4032 Debrecen, Hungary)

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Summary

When exposed to predators animals often benefit from synchronized movements and behaviour. In this study, we investigated the level of synchronization at arrivals at and departures from a feeding platform in flock-feeding tree sparrows (*Passer montanus*) under two different conditions; near to a protective cover or far from it. Sparrow flocks spent 43% less time in a feeding bout, and waited 30% more between bouts, far from the cover than near to it. The relationship of vigilance and flock size was different between the two conditions; the proportion of time allocated to vigilance increased more with decreasing flock size when far from the cover than when near to it. These results suggest that sparrows perceived higher predation risk when fed farther away from the protective cover. Furthermore, we found that far from the cover arrivals of sparrows were 79% more synchronized than when close to the cover. Finally, we did not find significant difference between the two feeding conditions in the synchronization at the departure. Possibly, due to its escape function, departures may be as synchronized as possible, even when feeding near to the protective cover.

Keywords: synchronized behaviour, predation risk, foraging, tree sparrow.

1. Introduction

In order to attain their energetic requirements, animals are often constrained to forage under considerable risk of predation (e.g., Walther & Gosler, 2001; Makowska & Kramer, 2007). When feeding under predation risk, birds may adopt several behavioural strategies in order to reduce the chance of being preyed upon. For instance, flocking is considered to be evolved — at least

[1] Corresponding author's e-mail address: monusf@delfin.unideb.hu

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partly — due to its anti-predatory benefits (reviewed by Beauchamp, 2002; Krause & Ruxton, 2002); and it was repeatedly shown that members of larger groups face lower predation risk (Foster & Treherne, 1981; Cresswell, 1994; Hebblewhite & Pletscher, 2002).

To some extent, group foragers synchronize their movements to maintain group cohesion, and the extent of group cohesion has a relevant role in the anti-predatory defence (Humphries & Driver, 1967; Carere et al., 2009). However, members of the flock frequently initiate or terminate feeding sequentially (Lima, 1988a; Rita et al., 1997; Barta et al., 2004). Members of flocks of the same size may experience lower effective flock size if they arrive at or leave a food patch sequentially than when they do it synchronously. Furthermore, benefits of flocking may be unevenly distributed among individuals if they arrive or leave asynchronously. For example, members initiating feeding earlier than their flock mates may experience much lower flock size and, hence, face a higher predation risk than individuals arriving later (Hegner, 1985; Lima, 1988b).

As synchronized behaviour was repeatedly observed in group-living prey animals and was assumed to be advantageous in avoiding predation (Humphries & Driver, 1967; Rodriguez et al., 2001; Carere et al., 2009), we hypothesized that group foragers initiate or terminate feeding more synchronously when they are more exposed to their predators. It was shown by earlier works (e.g., Pöysä, 1994; Lima et al., 1999), including one using the same species and the same experimental setting as the present study (Barta et al., 2004), that birds foraging farther from the shelter perceive themselves to be at higher risk. Therefore, we observed tree sparrow (*Passer montanus*) flocks feeding either near to or far from a bushy shelter in an environment where both aerial and terrestrial predators were present, and, in order to test our hypothesis, we investigated the degree of synchronization of arrivals and departures of the individuals in the two conditions.

2. Material and methods

2.1. Study site

The study was conducted in the Botanical Garden of the University of Debrecen, Debrecen, Hungary. The Garden is mainly an open, bushy area of 0.12 km^2. During the winter approximately 200–300 tree sparrows regularly forage there in flocks of various size (range 1–70; Z. Barta & F. Mónus, personal observation). Sparrowhawks (*Accipiter nisus*) and feral cats (*Felis silvestris catus*) are common visitors in the Garden, and both were observed attacking and capturing tree sparrows in the study site (Z.B. & F.M., personal observation). For a more detailed description of the study site, tree sparrows and their predators in the Garden see Barta et al. (2004).

2.2. *Experimental procedure*

We video recorded the behaviour of sparrows on a feeding platform on ten days in February of 2002. The platform was 150 × 150 cm and contained 144 holes arranged in a 12 × 12 grid, out of which 10 randomly chosen holes contained food during the experiments (see Barta et al., 2004). The edge of the platform was placed either 0.5 m (near condition) or 2.0 m (far condition) from the closest bush. Sparrows initiated feeding bouts from this bush, and returned there after the bouts.

We divided experimental days into seven time periods from dawn to dusk. Each time period included two separate recordings of 30 min, referred to as stages. The two stages within each time period were randomized between the near and far conditions. We recorded 7 × 2 stages per day, 140 stages altogether. During recordings the camera was mounted on a tripod, and we were concealed in a remote location in order to eliminate the effect of the experimenters. The camera recorded the whole surface of the platform and its very close proximity.

2.3. *Data collection*

Sparrows initiated feeding bouts in 118 out of the 140 stages. A feeding bout was defined as a separate event during which at least one sparrow resided on the platform, regardless whether they fed or not. We analysed two randomly chosen bouts per stage. We included only those bouts when at least ten sparrows stayed on the platform, resulting in 222 bouts analysed in detail. We chose the bouts in this manner in order to measure arrival dynamics using the first five and the first ten birds (see below).

We measured the length of each bout, defined as the time between the first arrival and the last departure. Arrival and departure of individuals was the moment when their legs touched or left the platform. For each bout, we recorded the maximum number and the mean number of sparrows staying on the platform, referred to as maximum flock size and mean flock size, respectively. The maximum flock size was directly measured from each bout, while the mean flock size was calculated as the mean of six different counts evenly distributed throughout the bout (a preliminary analysis on 20 random bouts showed that it gives a good estimation). We also measured the time between the actual bout and the one preceding it (time lag between bouts) as well as the duration of the preceding bout (except for the first bout of each stage).

To assess the degree of synchronization at arrival, we used the reciprocal of the time elapsed between the fifth and the tenth arrival. This variable deals with the potential confounding effect arising from the fact that the sparrows arriving first frequently fed alone for a disproportionately long time, while flock members arrived apparently more continuously after the arrival of the second or the third sparrow. We also calculated the expected arrival rate for each bout, as the maximum number of individuals during the bout divided by the duration of the bout. Thus, expected arrival rate shows the number of arriving sparrows per second provided that they arrive independently to each other. The degree of synchronization at the departure was defined as the reciprocal of the time elapsed between the departure of the first and the last bird. Note that birds always left the platform suddenly; therefore, the beginning and the end of the flock departure was unambiguous.

In the case of three randomly chosen sparrows per bout we measured the time they continuously spent on the platform, and we counted the video frames on which the sampled bird's head was in head-up position as in Barta et al. (2004). We defined the proportion of time allocated to vigilance for each bout as the sum of times the three individuals spent in head-up position divided by the sum of times they spent on the platform.

2.4. Data analysis

Statistical tests were carried out in the R statistical environment (R Development Core Team, 2009). Data were analysed by fitting linear mixed effects models (*lmer* function in R; Bates & Sarkar, 2005). In this type of analyses fixed effect variables are analysed as if the effects of all previously entered variables (confounding variables) were statistically controlled for. These models increase the validity of results, as they take into account the random variance component arising from the diversity of samples, and allow for handling repeated (correlated) measures (Zar, 1984). In our study, subsequent observations were unlikely to be independent from each other, because of possible similarities between days, time periods or stages. In order to statistically eliminate potential pseudoreplications deriving from this data structure, we used a hierarchical design of random effects (days, time periods within days and stages within time periods). This statistical design also deals with the possibility that subsequent bouts during stages may be observations made on the same flocks. However, observations made on individually colour-ringed birds during a previous study make it highly unlikely that our results are based on a few oddly behaving individuals (see Barta et al., 2004).

In the cases of log-normally distributed variables (time measurements), we analysed the log transformed data. In the cases of normally distributed variables (proportion of time allocated to vigilance, number of bouts per stage, maximum and mean flock size) we analysed the untransformed data. Mean $\pm$ SE of original data is shown in the latter cases, while for log-normal variables back-transformed values of the mean and the range of mean $\pm$ SE of the transformed values are shown (Zar, 1984).

3. Results

3.1. Feeding behaviour

Neither maximum flock sizes nor mean flock sizes differed between the near and the far condition (Table 1). Under the far condition sparrow flocks initiated significantly more, but shorter bouts; individuals also spent significantly less time on the platform during feeding bouts (Table 1). The time lag between the bouts decreased as the mean flock size increased ($\chi^2_1 = 5.035$, $p = 0.025$). Sparrows waited more prior to initiating a new bout under the far condition; time lags were significantly longer than those under the near condition (Table 1). The time lag was not affected by the duration of the previous bout (after controlling for mean flock size and feeding condition: $\chi^2_1 = 0.203$, $p = 0.652$).

The proportion of time allocated to vigilance increased significantly as the mean flock size decreased (Figure 1; $\chi^2_1 = 21.803$, $p < 0.001$). Vigilance increased more steeply with decreasing flock size when far from the cover than when near to it, as revealed by the significant interaction between mean flock size and the distance to the cover (Figure 1; $\chi^2_1 = 5.437$, $p = 0.020$).

Table 1. The effect of distance to the shelter on the measured variables in the case of group-feeding tree sparrows.

Variable	Mean (SE)		Test statistics	
	Near to cover	Far from cover	χ_1^2	p-value
Maximum flock size	24.4 (23.39–25.41)	23.3 (22.55–24.05)	0.646	0.422
Mean flock size	19.4 (18.48–20.32)	19.5 (18.83–20.17)	0.016	0.900
Duration of flock's bouts (s)[a]	18.2 (16.78–19.85)	10.3 (9.53–11.14)	22.773	<0.001
Duration of individual bouts (s)[a]	11.7 (10.92–12.51)	7.9 (7.39–8.36)	19.065	<0.001
Number of bouts per stages	11.7 (10.67–12.73)	17.0 (15.73–18.27)	11.336	<0.001
Proportion of time in vigilance	0.34 (0.332–0.348)	0.35 (0.342–0.358)	1.025	0.311[b]
Time lag between bouts (s)[a]	13.3 (12.21–14.41)	17.3 (15.93–18.69)	4.452	0.035[b]
Expected arrival rate (1/s)[a]	1.15 (1.041–1.266)	2.10 (1.948–2.264)	18.724	<0.001
Synchronization at arrival (1/s)[a]	1.75 (1.486–2.079)	3.13 (2.762–3.497)	9.970	0.002[c]
Synchronization at departure (1/s)[a]	3.33 (3.155–3.436)	3.448 (3.356–3.636)	0.712	0.399[b]

Test statistics are from the mixed effect linear models.

[a] Log-normally distributed variables; means and SEs were calculated as indicated in section 2.4.

[b] After controlling for flock size (mean flock size, but maximum flock size in the case of synchronization at departure; see Section 3.2).

[c] After controlling for expected arrival rate, mean flock size, length of previous bout and the time lag preceding the actual bout.

3.2. *Synchronization*

As expected, the degree of synchronization at arrival increased as the expected arrival rate increased ($\chi_1^2 = 56.123$, $p < 0.001$). Furthermore, sparrows arrived to the feeding platform more synchronously as mean flock size increased (after controlling for expected arrival rate: $\chi_1^2 = 11.518$, $p < 0.001$; Figure 2a), as the length of the previous bout increased (after controlling for expected arrival rate and mean flock size: $\chi_1^2 = 100.77$, $p < 0.001$), as the length of the time lag preceding the bout decreased (after controlling for expected arrival rate, mean flock size and length of previous

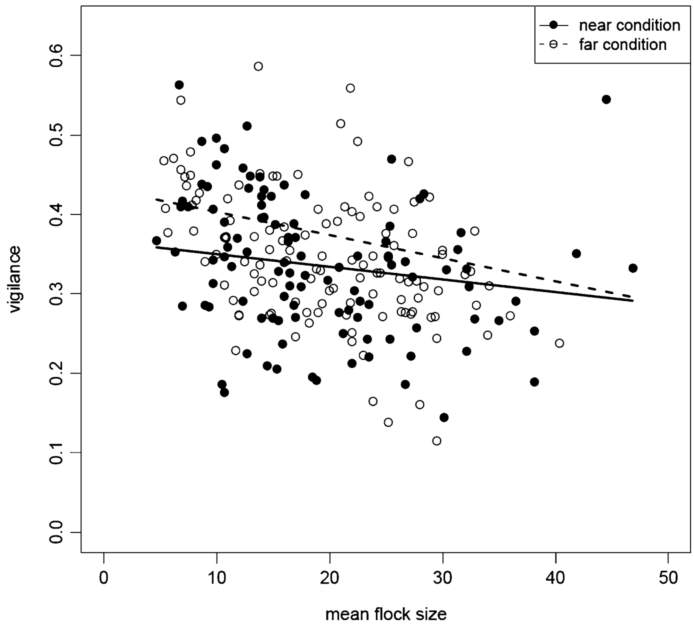

Figure 1. The proportion of time allocated to vigilance in relation to flock size in tree sparrow flocks foraging near to and far from a shelter. Lines are predicted regression lines from the *lmer* model (for details, see Section 2.4).

bout: $\chi^2_1 = 12.082$, $p < 0.001$); as well as under the far condition (Table 1; Figure 2a). None of the investigated variables showed significant interaction with the distance to the cover ($p > 0.5$; for all cases). Note that the degree of synchronization was significantly higher under the far condition even without controlling for the abovementioned confounding variables ($p < 0.05$ for all cases).

The degree of synchronization at departure decreased as maximum flock size increased ($\chi^2_1 = 16.616$, $p < 0.001$; Figure 2b) and did not differ between conditions (Table 1; Figure 2b). In this latter analysis we used maximum flock sizes, because flock size usually peaked at the end of the bout; using mean flock sizes produced qualitatively similar results (not shown).

4. Discussion

In this study we investigated the degree of synchronization of arrivals at and departures from a food patch in winter flocks of free-living tree sparrows

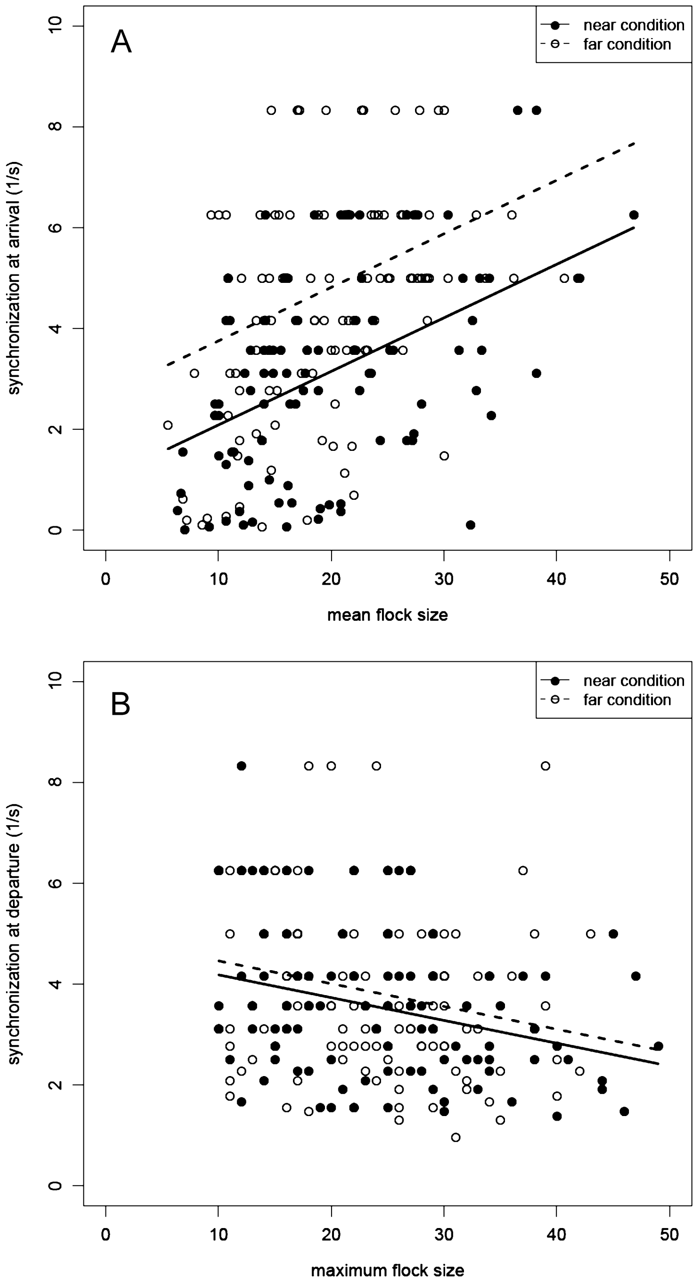

Figure 2. The degree of synchronization (a) at the arrival and (b) at the departure in relation to flock size in tree sparrow flocks foraging near to and far from a shelter. Lines are predicted regression lines from the *lmer* model (for details, see Section 2.4).

foraging near to and far from a bushy shelter. The findings that sparrows increased vigilance more with decreasing flock size, initiated shorter bouts and waited more between bouts under the far than under the near condition, indicate that they perceived the far condition as more risky. Sparrows initiated more feeding bouts far from the shelter suggesting that they attempted to compensate for lost feeding time originating from shorter bouts. This excludes the possibility that they reduced the length of feeding bouts due to energetic considerations. As initiation of more bouts definitely requires larger energy expenditure, it is very likely that sparrows were compelled to behave in this manner, possibly by higher perceived risk. Similarly, we found in a former study performed at the same site that the risk perceived by tree sparrows was higher at 2.0 m than at 0.5 m distance to the cover; and sparrows were unwilling to forage when the feeding platform was placed even farther from the shelter (see Barta et al., 2004).

Sparrows arrived at the platform nearly twice as more synchronously far from than near to the cover. This increased synchronization may be due to several reasons in our study. Highly synchronized arrivals may have antipredatory benefits, as more individuals take part of the risk resulting in a greater effective group size. This may enhance the dilution effect (Foster & Treherne, 1981) or, under an attack of a predator, the confusion effect (Humphries & Driver, 1967; Carere et al., 2009). In accordance, Hegner (1985) and Lima (1988b) found that flock members initiating feeding earlier at dawn dedicated more time to vigilance than flock mates arriving later, presumably because the formers perceive higher predation risk. More synchronized arrival may allow for more efficient exploitation of a food patch during limited time, because more birds may forage during almost the whole duration of the bout. In accordance, in our study the duration of individual's feeding bouts under the far condition decreased less than the duration of flock's feeding bouts (32% and 43% decrease, respectively) as compared to the near condition. One may argue that higher degree of synchronization may also result from the shorter length of feeding bouts under the far condition i.e., more individual arrive during a shorter time. On the other hand, the effect of treatment on synchronization remains after controlling for expected arrival rate.

Higher degree of synchronization as well as shorter bouts under the far condition may be explained also by the increased number of false alarms, i.e., individuals may hurry to resume foraging after false alarms (see Hegner, 1985). However, we found the time lags between feeding bouts not shorter but even longer, under the far condition, making this explanation unlikely. A hurry to resume feeding may explain why sparrows synchronized more their arrivals after longer previous bouts and after shorter time lags between bouts. However, this phenomenon did not affect our main result, because the difference between conditions in the degree of synchronization remained well marked after controlling for these variables.

Alternatively, higher degree of synchronization far from the cover may be due directly to the greater flying distance or the flatter flying angle when flying farther from the bush. As to now, the rules individuals use in order to achieve synchronization or avoid collision when flying in groups are poorly understood (Ballerini et al., 2008a,b; Bajec & Heppner, 2009). However, as the difference in the covered distances in our study is short, it seems unlikely to affect flying properties as much as to induce a change of this magnitude in synchronization.

In contrast to arrivals, the degree of synchronization of departures did not differ between the far and the near conditions. Departures passed off very quickly (approximately 0.3 s by average) and were equally highly synchronized regardless of the distance to the cover. Apparently, they act as an escape flight, and may be as synchronized as possible. Former studies investigating how individuals achieve synchronized escape flight suggest that the level of synchronization may be limited, e.g., by flock size (see in Hilton et al., 1999). In accordance, the degree of synchronization at departure decreased with increasing flock size in our study. However, the inverse relationship we found between synchronization and flock size at the arrivals may only be explained speculatively. Additional studies aiming to understand explicit rules shaping synchronized behaviours (e.g., Ballerini et al., 2008a,b) are needed to enhance our knowledge on collective behaviour.

Though synchronization may carry many advantages, in certain situations early or late arrival of individuals may be more beneficial. Hungry birds may be more willing to initiate foraging (e.g., Koivula et al., 1995; see also Lima, 1988a; Lahti et al., 1997 for the feeding initiation at dawn), while birds joining later to their flockmates spend less time exposed to predators. Early arrival may also be beneficial for individuals playing producer (see producer–scrounger game; Barnard & Sibley, 1981; Giraldeau & Caraco, 2000). Integrated investigation of individual and group-level cost and benefits of synchronization within a common framework remains the task for future studies.

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