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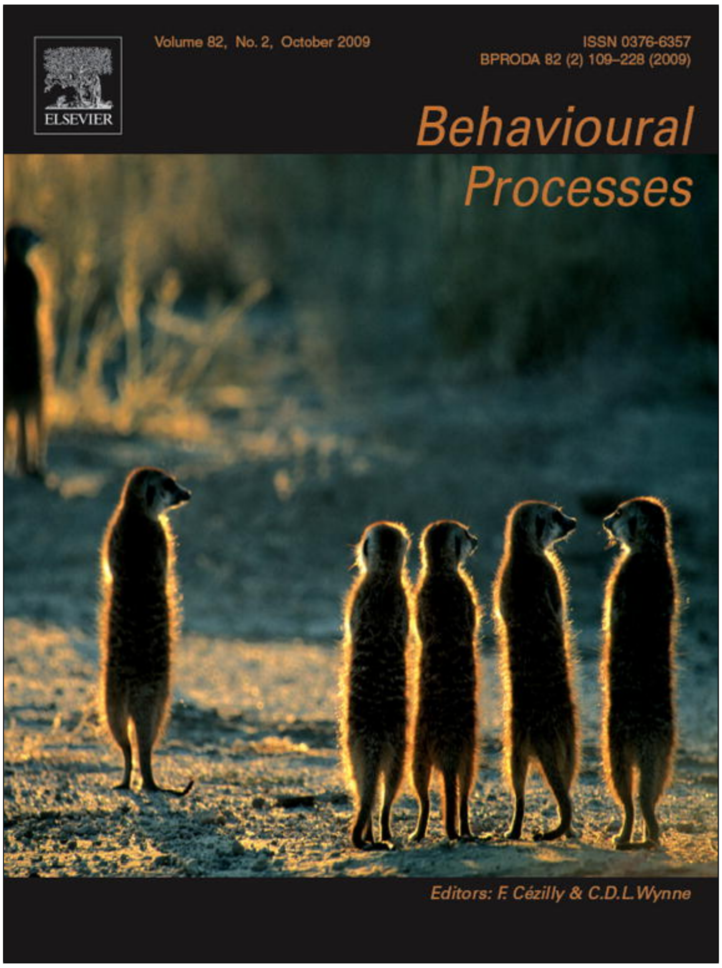
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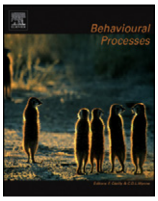

# Whom do the sparrows follow? The effect of kinship on social preference in house sparrow flocks

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## ABSTRACT

Non-aggressive social interactions between group-mates, e.g. maintenance of spatial proximity or activity synchrony are basic elements of a species' social structure, and were found to be associated with important fitness consequences in group-living animals. In the establishment of such affiliative relationships, kinship has often been identified as one of the key predictors, but this has rarely been studied in simple social groups such as flocks of gregarious birds. In this study we investigated whether kinship affects social preference, as measured by the tendency to associate with others during various social activities, in captive house sparrow (*Passer domesticus*) flocks where birds could interact with differently related flock-mates. We found that preference between flock-mates was correlated with familiarity from early nestling period: same-brood siblings followed their sib initiating new activities more often than non-sib birds. The strength of association between birds also tended to correlate with genetic relatedness, but this was mainly due to the effect of siblings' affiliation. Thus we concluded that house sparrows prefer the company of their siblings during social activities even well after fledging, which may facilitate kin-biased behaviours.

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## 1. Introduction

In species living in social groups, individuals can interact both agonistically and socio-positively with their companions, and these interactions create the basis of the interdependent levels of the species' social structure. Affiliative relationships between individuals have been observed in many animal taxa, e.g. in the form of spatial proximity (Burley et al., 1990; Gowans et al., 2001), activity synchrony (Casinello and Calabuig, 2008), social support (Weiss and Kotrschal, 2004; Whitehead and Connor, 2005) or particular behaviours like grooming (Mitani et al., 2000) and allopreening (Stamps et al., 1990). These interactions are important and receive considerable attention because of their various fitness consequences, e.g. social support in Siberian jays (*Perisoreus infaustus*) enhances the survival of retained offspring (Ekman et al., 2000), grooming in primates can be exchanged for food (de Waal, 1989) or protection against harassment (Silk, 1982). Furthermore, affiliative interactions may also contribute to the development and patterns of socially facilitated behaviours such as exploration (Stöwe et al., 2006; Scheid et al., 2007) and social learning (Smith et al., 2002; Schwab et al., 2008). Kinship has been found to influence affiliative relationships in many primates (see in Silk, 2002) but also in other vertebrate species including birds (Stamps et al., 1990; Parker et al., 1995; Rossiter et al., 2002; Parsons et al., 2003; Ward and Hart, 2003), indicating that kin companions often spend more time close together or sustain smaller inter-individual distances. Even in species that are not characterized by prolonged family bonds and whose group formation is not primarily based on genetic relatedness, preference for kin companions may emerge (e.g. Burley et al., 1990). Kin-biased behaviour is expected to evolve only when (1) it entails an overall fitness gain to the individuals (either directly or indirectly through the benefit of kin companions) and (2) at least a few kin group-mates are present that individuals are able to distinguish from non-kin. If these conditions are met, members of species that live in relatively simple social groups (in the sense that they apparently lack kinship-structure) may also take relatedness into account during social activities, which can considerably affect the pay-offs of different social interactions between group-mates. Despite of this potential importance of the relationship between relatedness and social behaviours, it has been investigated very scarcely in simple social groups that are widespread in the animal kingdom.

In this study we investigated social preferences in winter flocks of house sparrows (*Passer domesticus*). Sparrows are highly gregar-

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ious, they form flocks during the non-breeding season that consist of 10–30 or more individuals, and flock-members perform various activities together such as foraging, roosting and dust-bathing (Anderson, 2006). Our analyses of relatedness in free-living winter flocks (Liker et al., submitted manuscript) and also the high inbreeding found in the wild (although in island populations; Jensen et al., 2007) indicate that most sparrows have at least a few close relatives in their flocks, yet little is known of the role of kinship in their social interactions. A recent study found that sparrows show distinct behaviour toward their relatives during social foraging: they use the aggressive form of scrounging (exploiting other's food findings) less often and obtain less food by that tactic from their close kin than from unrelated birds (Tóth et al., 2009a). Despite the fact that the house sparrow has long been a "model species" for studies on various social phenomena such as dominance hierarchy, social foraging and social learning (Anderson, 2006), according to our knowledge, affiliative interactions and the possible significance of kinship in such interactions have never been investigated in the species.

To test whether kinship affects social preference in house sparrows, we observed captive flocks in which birds could interact with differently related individuals. Specifically, we tested whether (1) preference between sparrow flock-mates or in sex-specific dyads increases with genetic relatedness and (2) same-brood siblings maintain stronger affiliations with each other than non-sib dyads. As a sign of preference for specific individuals and thus as a basic measure of affiliation, we studied within-group 'following events' in which birds engaged into different social activities by joining a flock-mate.

## 2. Materials and methods

### 2.1. Study subjects

We captured house sparrows with mist nets in the early post-breeding periods (mostly September) of 2005–2006 in the Kittenberger Zoo in Veszprém, Hungary, where we have been studying the sparrow population since 2004. As we had monitored the breeding of ringed birds and also ringed the nestlings, we had pedigree information for many individuals by the time of capture. We allocated the captured birds into two flocks in 2005 and formed one flock in 2006, so that each contained same-brood siblings (Table 1). All siblings and most other birds were juveniles of the year (49 out of the 61 individuals). Upon capture we measured body mass (±0.1 g), took small blood samples (approx. 100 μl) for kinship analyses, and ringed each individual with a numbered aluminium ring and three colour rings. Birds were held in outdoor aviaries (approx. 5 m ($W$) × 4 m ($L$) × 3 m ($H$)). In 2005 flocks 1 and 2 were held separately in two aviaries, which were ca. 5 m apart, with partial visual barriers (bushes) between them. Housing arrangements were identical in both years and for each flock: we provided roosting trees and small boxes for sleeping and resting, *ad libitum* water and food (millet, oat, wheat, and sunflower seeds), and we regularly added multivitamin droplets to the water. Observations took place after a 4-week long acclimatization period, and lasted 2–3 months (Table 1), after which we released all birds at the site of capture. None of the birds studied in 2005 was re-used in flock 3 in 2006. For further details on the captive flocks, see Tóth et al. (2009a,b).

### 2.2. Measuring relatedness

Blood samples were obtained from the brachial vein of captured birds, as a standard for blood-taking in small passerines (e.g. Jensen et al., 2003), and were stored in Queen's lysis buffer (Dawson et al., 1998) until analysis. DNA extraction from the blood samples was performed with standard phenol-chloroform procedure, or with Qiagen DNeasy Tissue Kit, following the producer's instructions. Seven highly polymorphic microsatellite loci were used for genotyping (allele numbers: 13.29 ± 0.78; for details about allele sizes and frequencies see electronic Appendix in Tóth et al., 2009b). Primers for four dinucleotide loci (*Pdo1*, *Pdo2* [Neumann and Wetton, 1996], *Pdo5* [Griffith et al., 1999] and *Pdo8 mu* [Griffith et al., 2007]), one trinucleotide locus (*Pdo9*, Griffith et al., 2007) and one tetranucleotide locus (*Pdo3*, Neumann and Wetton, 1996) were developed specifically for house sparrows. Another dinucleotide locus (*McyU4*) was originally isolated for the superb fairy-wren *Malurus cyaneus* (Double et al., 1997), and was used successfully in genetic studies of sparrows (e.g. Jensen et al., 2003). In each primer pair (Sigma–Aldrich Ltd., Budapest, Hungary), forward primers were fluorescently labelled on the 5′-end with HEX, JOE or FAM-6 dyes (Applied Biosystems Inc.). PCR reactions consisted of approximately 100 ng of template DNA, 0.5 μM of each primer, 0.2 mM dNTPs, 2 mM $MgCl_{2,}$ 1 unit of Taq DNA polymerase (Fermentas Inc. Vilnius, Lithuania) and the 10X Taq buffer in a final volume of 25 μl. To resolve alleles, all amplified PCR products were analyzed on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems Inc.) at the Biomi Ltd. (Gödöllő, Hungary) using ROX-labelled ILS-600 internal standard (Promega Corp. Madison, Wisconsin, USA). The data were analyzed with the GeneScan software (Applied Biosystems Inc.).

ML-Relate computer program (Kalinowski et al., 2006) was used to calculate maximum likelihood estimates of relatedness between individuals from genotypic data. This method accommodates null alleles during the estimations which had high frequency at two loci (*Pdo2*: 0.20, *Pdo8*: 0.18), and is considered to be more accurate

**Table 1**
Characteristics of the studied house sparrow flocks.

| | Flock 1 | Flock 2 | Flock 3 |
|---|---|---|---|
| Study period | October–December 2005 | October–December 2005 | October–November 2006 |
| Number of sampling periods (h) | 8 | 13 | 29 |
| Number of individuals | 21 | 23 | 17 |
| Males | 14 | 11 | 10 |
| Females | 7 | 12 | 7 |
| Number of same-brood siblings | 9 (3 dyads, 1 triad) | 10 (3 dyads, 1 tetrad) | 10 (5 dyads) |
| Number of observed followings (Number of dyads): | | | |
| Flock total | 80 (420) | 138 (506) | 250 (272) |
| Male:male | 34 (182) | 54 (110) | 91 (90) |
| Male:female | 20 (98) | 31 (132) | 52 (70) |
| Female:female | 10 (42) | 19 (132) | 43 (42) |
| Female:male | 16 (98) | 34 (132) | 64 (70) |
| Sibling dyads | 6 (12) | 12 (18) | 17 (10) |
| Non-sibling dyads | 74 (408) | 126 (488) | 233 (262) |
| Per individual (mean ± SE) | 4.21 ± 0.49 | 6.0 ± 0.55 | 14.71 ± 1.19 |

than other estimators (Milligan, 2003). We performed estimations of allele frequencies and pair-wise genetic relatedness by entering all individuals' genotype in the program as if they were a single population, since no prior reference data was available about the studied sparrow population.

### 2.3. Measuring associations between individuals

Behavioural observations took place between 8:00 and 17:00 h, in randomly distributed 1-h long sampling periods. During these observations, through a one-way window we recorded all pair-wise 'following events' in which both participants were unambiguously recognizable. We defined following as an event when an individual started a new activity (e.g. switched from roosting to feeding) by following an initiator flock-mate. The former participant was described as "follower", while the latter as "initiator". Only those following events were taken into account in which the follower bird both followed the initiator within 5 s and arrived within 0.5 m to it, and the participants showed no aggression toward each other, as our aim was to measure affiliative relationships between flock-mates. Birds followed each other to different roosting and resting places (29% of the total number of following events), to the feeder (37%), to the drinking bowl (10%) or to dust-bathing spots (24%). We calculated pair-wise association indices from following events and used them in the further analyses. Since flock-mate following was an asymmetric behavioural measure (the number of events in which A followed B is usually not identical to the number of events in which B followed A), the calculated association indices were unidirectional (Whitehead et al., 2005). We expressed the degree of association of an individual to its flock-mate by the number of times the individual followed that particular bird, and computed 'half-weight' association indices according to Cairns and Schwager (1987), and following the recommendations of the SOCPROG 2.3 program manual (Whitehead et al., 2005).

### 2.4. Statistical analyses

We applied two different approaches to investigate the relationship between relatedness and association indices. First, we tested whether the strength of association between birds was correlated with the degree of their genetic relatedness. To this end, we calculated a matrix of pair-wise genetic relatedness coefficients ($r_{ML}$) from the ML-Relate estimations for each flock, and correlated it with a matrix of pair-wise association indices. Second, we tested whether siblings were more associated than non-sib birds. Here we correlated the matrix of association indices with another matrix that coded the relationship between individuals as 1 if they were known to be same-brood siblings and as 0 if they were not sibs according to our pedigree data (Table 1). For all analyses we applied Hemelrijk's (1990b) $K_r$ test that is a variant of the Mantel (1967) test for matrix correlation that takes individual variation in behaviour into account. This test has often been used in similar studies, where the relationship between pair-wise associations and kinship was investigated (e.g. Goldberg and Wrangham, 1997; Mitani et al., 2000). Additionally, we also performed $K_r$ tests for each combination of the initiator's and follower's sex to detect potential sex-specific effects in the relationship of genetic relatedness and association indices. Furthermore, partial Mantel-tests were used to investigate the correlation between relatedness and association indices while controlling for early familiarity (i.e. whether the members of a dyad were siblings or not). Indices of association were calculated and all matrix permutation tests were performed in the compiled version of SOCPROG 2.3 program, written for the analysis of animal social structure (Whitehead et al., 2005). In all tests one-tailed probability values were calculated (according to Hemelrijk, 1990a) based on 10,000 iterations. Since tests were performed for the three flocks separately, we adjusted the statistical criterion of significance using sequential Bonferroni-correction (Sokal and Rohlf, 1995). Additionally, we applied one-tailed Approximative Spearman Correlation Test ('coin' package for R; Hothorn et al., 2008) to test reciprocity of sib preference within sibling dyads, using R statistical program (R Development Core Team, 2005). We applied this test with Monte Carlo resampling as we allowed for the fact that dyads within the sibling triad and tetrad were not independent from each other. We divided all sibling dyads into a 'more eager to follow (A)' and a 'less eager to follow (B)' member according to their association indices, then examined the correlation between them. If the degree of association of A to B is correlated with that of B to A, the association is considered to be reciprocal, otherwise it is said to be unidirectional (Hemelrijk, 1990b).

**Table 2**

Pair-wise association indices and genetic relatedness between followers and initiators, and the probability of the correlation between association index and relatedness in three house sparrow flocks.

| Flock | Dyads (*N*) | Association index (mean ± SE) | $r_{ML}$[a] (mean ± SE) | *P*[b] |
|---|---|---|---|---|
| 1 | All (420) | 0.05 ± 0.01 | 0.05 ± 0.01 | $P = 0.072$ |
| | Male–Male (182) | 0.04 ± 0.01 | 0.05 ± 0.01 | $P = 0.094$ |
| | Male–Female (98) | 0.04 ± 0.01 | 0.06 ± 0.01 | $P = 0.785$ |
| | Female–Female (42) | 0.07 ± 0.03 | 0.08 ± 0.02 | $P = 0.233$ |
| | Female–Male (98) | 0.05 ± 0.01 | 0.06 ± 0.01 | $P = 0.154$ |
| 2 | All (506) | 0.04 ± 0.004 | 0.06 ± 0.01 | $P = 0.681$ |
| | Male–Male (110) | 0.06 ± 0.01 | 0.08 ± 0.02 | $P = 0.045$ |
| | Male–Female (132) | 0.04 ± 0.01 | 0.02 ± 0.005 | $P = 0.616$ |
| | Female–Female (132) | 0.03 ± 0.01 | 0.09 ± 0.01 | $P = 0.901$ |
| | Female–Male (132) | 0.04 ± 0.01 | 0.02 ± 0.005 | $P = 0.633$ |
| 3 | All (272) | 0.06 ± 0.004 | 0.06 ± 0.01 | $\boldsymbol{P = 0.009}$ |
| | Male–Male (90) | 0.07 ± 0.01 | 0.07 ± 0.02 | $P = 0.461$ |
| | Male–Female (70) | 0.06 ± 0.01 | 0.04 ± 0.01 | $P = 0.056$ |
| | Female–Female (42) | 0.06 ± 0.01 | 0.12 ± 0.03 | $P = 0.678$ |
| | Female–Male (70) | 0.05 ± 0.01 | 0.04 ± 0.01 | $\boldsymbol{P = 0.003}$ |

[a] Genetic relatedness ($r_{ML}$) was estimated by maximum likelihood method.

[b] One-tailed *P*-values are based on $K_r$ tests and derived from 10,000 iterations. Correlations that remained statistically significant after sequential Bonferroni-correction are shown in bold.

## 3. Results

Genetic relatedness significantly correlated with association indices between flock-mates in 1 out of 3 flocks (Table 2). However, in the partial Mantel-tests controlling for the presence of sibling dyads, there was no correlation between genetic relatedness and pair-wise association indices in any flock (flock 1: $r = 0.018$, $P = 0.339$; flock 2: $r = -0.062$, $P = 0.922$; flock 3: $r = -0.026$, $P = 0.631$). These findings were supported by sex-specific analyses: the correlation of relatedness and association indices was not significant in any case, except that females followed their male kin more often than less closely related males in flock 3 (Table 2).

On the other hand, siblings in all flocks tended to be more closely associated than non-sib flock-mates (Fig. 1), and this tendency was significant in two out of three flocks (flock 1: $P = 0.056$; flock 2: $P = 0.011$; flock 3: $P = 0.009$; Fig. 1). Note that the highest number of followings were observed in flock 3 whereas the fewest in flock 1 due to varying sampling effort (Table 1). Sex-specific association between siblings were not analysed because of low sample sizes.

Pair-wise association indices within sibling dyads were correlated with each other ($Z = 2.902$, $N = 20$, $P = 0.001$), indicating that preference for sib flock-mates was reciprocal.

## 4. Discussion

In this study we investigated how kinship affects social preference in winter flocks of house sparrows. We found that genetic

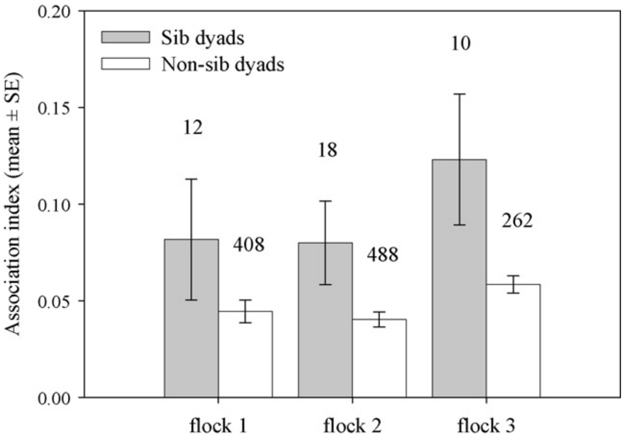

**Fig. 1.** Half-weight association indices of sib and non-sib dyads. Sib dyads are same-brood siblings, non-sib dyads are all other pairs of birds in the flock; values above bars represent the number of dyads in each category.

relatedness in itself had little effect on social preference, but sibling birds were more associated than non-sib individuals. Although the latter relationship did not reach statistical significance in one out of three flocks, we suggest this was most likely due to lower power (smaller sample size) in that flock, as the observed trend was similar in all flocks (Fig. 1). Based on data from three flocks and 2 years, our results demonstrate a clear trend for social preference among sibling companions, indicating that house sparrows can discriminate their siblings during social behaviours several months after fledging.

So far only a few studies investigated how kinship may affect various aspects of social interactions in species that live in social groups not characterized by the high frequency of closely related group-mates. For example, Burley et al. (1990) tested adult zebra finches (*Taeniopygia guttata*) for their tendency to perch with differently related and/or familiar individuals. Although the aggregation of kin individuals is not typical in that species (Zann, 1996), Burley et al. (1990) found that males preferred the proximity of their male siblings whereas females showed preference for male first-cousins, irrespective of prior familiarity. The wintering flocks of house sparrows are typically formed after the dispersal period by large post-breeding flocks breaking apart into smaller resident groups (Anderson, 2006) that contain relatively few kin dyads (Liker et al., submitted manuscript). Still, according to our present results, kinship influences affiliative relationships within such flocks, as sparrows seem to prefer following their sibs during social activities (note that the proportion of close kin within our captive flocks was very similar to what we observed within free-living wintering flocks, i.e. 14–15%). Sparrows may profit from the proximity of their relatives in several ways. First, sib preference may be beneficial in terms of social foraging: we previously found that sparrows avoid aggressive exploitation of their close kin (including siblings) during social foraging (Tóth et al., 2009a), thus feeding in the proximity of sibs may reduce the likelihood of being scrounged by neighbours. Second, social preference for siblings may also be related to social facilitation and learning. Sparrows often use public information, i.e. social cues provided by their flock-mates in their decisions such as where and what to eat (Elgar and Caterall, 1982; Turner, 1964; Fryday and Greig-Smith, 1994). Individuals may preferentially use their sibs as sources of information about the environment and/or benefit from their sibs' exploratory behaviour by frequently following them if information transfer is more efficient between siblings than among non-sib individuals, as has been demonstrated in ravens (*Corvus corax*) by Schwab et al. (2008). Thirdly, sib preference may be a "carry-over" effect from the post-fledging period, when simply by following their siblings young birds could increase the chance of obtaining food from their parents or reduce the risk of predation. A recent study has shown that early filial experiences may shape sparrows' preferences for certain tactics during social foraging (Katsnelson et al., 2008). In a similar way, young sparrows might learn to "copy" their siblings' behaviour (e.g. to follow them to shelter or to feeding sites).

In conclusion, we suggest that house sparrows maintain a more affiliative relationship with their same-brood siblings in non-breeding flocks even months after the post-fledging period. This result is interesting not only because no affiliative behaviour has been described in house sparrow flocks previously, but also because it demonstrates kin preference in a simple, not kin-based animal group. Our work indicates that this sib preference may be beneficial during social foraging (Tóth et al., 2009a). Future studies should test the fitness consequences (e.g. social facilitation and learning) and the proximate mechanisms of sib preference (e.g. by separating the effects of genetic relatedness and familiarity) in this highly social species.

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