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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.

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