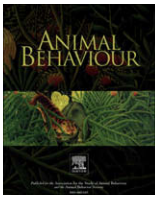
Animal Behaviour 77 (2009) 337–342

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe



Effects of relatedness on social-foraging tactic use in house sparrows

Zoltán Tóth [a,*], Veronika Bókony [a], Ádám Z. Lendvai [b,1], Krisztián Szabó [c,2], Zsolt Pénzes [c,d,3], András Liker [a]

[a] Department of Limnology, University of Pannonia
[b] Institute of Biology, College of Nyíregyháza
[c] Institute of Genetics, HAS Biological Research Center, Szeged
[d] Department of Ecology, University of Szeged

ARTICLE INFO

Article history:
Received 11 February 2008
Initial acceptance 8 April 2008
Final acceptance 2 October 2008
Published online 26 November 2008
MS. number: 08-00078R

Keywords:
genetic relatedness
house sparrow
kin discrimination
Passer domesticus
scrounging

Kin selection is often important in the evolution of reproductive behaviour, but we know much less about its significance for nonreproductive social groups. We investigated whether relatedness affects social-foraging behaviour in captive house sparrow, *Passer domesticus*, flocks, where birds may either search for food or exploit flockmates' food findings by scrounging. In such systems, both increased and decreased frequency of scrounging from relatives can be predicted by kin selection theory, depending on the relative costs and benefits of exploiting close kin. We found that birds used aggressive joining less often and obtained less food by that tactic from their close kin than from unrelated flockmates. In nonaggressive joinings, males also tended to join less often and obtained less food from close kin flockmates than from unrelated birds, whereas an opposite trend was found in females. Close kin males also spent less time feeding together from the same food patch than unrelated males, further suggesting reduced exploitation by male kin. These results suggest that house sparrows are able to recognize their close kin flockmates and reduce aggressive scrounging towards them, and that the sexes may differ in some forms of kin exploitation.

During group foraging, individuals may use alternative behavioural tactics, such as producing and scrounging, to maximize their own net energy intake: producers find their own food, while scroungers exploit food sources found by their groupmates (Barnard & Sibly 1981). Game-theoretical models showed that the use of these tactics in a group is frequency dependent and can be evolutionarily stable (e.g. Giraldeau & Caraco 2000), while empirical studies demonstrated that tactic use is influenced by ecological conditions such as predation (Coolen & Giraldeau 2003; Barta et al. 2004) and characteristics of the foragers, including their dominance rank (Caraco et al. 1989; Wiley 1991; Liker & Barta 2002), energy reserves (Lendvai et al. 2004) and early experience (Katsnelson et al. 2008).

A further factor that may affect the frequency of groupmate exploitation is the relatedness between foraging individuals. Kin selection theory predicts that, whenever the relatedness between two interacting individuals multiplied by the benefit of the helped individual exceeds the cost of the helper, kin-biased behaviour may evolve (Hamilton 1964). This theory has been successfully used to explain a variety of social behaviours both in reproductive (e.g. Komdeur 1994; Queller & Strassmann 1998) and nonreproductive contexts (e.g. Hatch & Lefebvre 1997; Hokit & Blaustein 1997; Sklepkovych 1997; Rossiter et al. 2002). Hamilton's (1964) rule predicts two alternatives of kin-favouring behaviour during social foraging, depending on the payoffs of scrounging and being exploited, respectively: (1) when the costs of scrounging are high for the exploited bird, individuals may help their kin by avoiding exploiting them (i.e. reduced scrounging from kin); (2) if the benefits of scrounging are high for the scrounger, birds may allow kin to feed from their food patches (i.e. increased scrounging from kin). In the absence of kin selection, however, no such difference is expected.

To our knowledge, only two studies have investigated the effects of relatedness on social foraging. Hatch & Lefebvre (1997) found that juvenile ringdoves, *Streptopelia risoria*, joined, nonaggressively, the food discoveries of their siblings and parents more often than those of unrelated adults. However, the authors interpreted these results in the context of cultural transmission and did not suggest a role for kin selection. In another study, Ha et al. (2003) found that in northwestern crows, *Corvus caurinus*, nonaggressive scrounging tended to occur between more closely related individuals and

---

[*] Correspondence: Z. Tóth, Department of Limnology, University of Pannonia, Egyetem u. 10, H-8201 Veszprém, Hungary.
E-mail address: tothzoltan81@yahoo.com (Z. Tóth).

[1] A. Lendvai is at the Institute of Biology, College of Nyíregyháza, Sóstói u. 31/b, H-4400 Nyíregyháza, Hungary.

[2] K. Szabó is at the Institute of Genetics, HAS Biological Research Center, Temesvári krt. 62, H-6701 Szeged, Hungary.

[3] Z. Pénzes is at the Department of Ecology, University of Szeged, Közép fasor 52, H-6701 Szeged, Hungary.

0003-3472/$38.00 © 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2008.10.005

aggressive scrounging among less closely related individuals, although crows did not preferentially steal, or avoid stealing, from relatives overall. Ha et al. (2003) suggested that scrounging behaviour could be affected by indirect fitness effects, although the interpretation of their results is complicated by the occurrence of cooperative breeding and extended parental care in this species (Verbeek & Butler 1999). Clearly, more studies are needed if we are to improve our understanding about how relatedness affects the exploitation of companions in foraging groups.

We investigated the effects of kinship on scrounging tactic use in one of the best known producer–scrounger systems, the house sparrow, *Passer domesticus*. Sparrows usually feed in flocks and use both producer and scrounger tactics to find their food (Barnard & Sibly 1981; Johnson et al. 2001; Liker & Barta 2002). Inbreeding is high in the wild (at least in island populations; Jensen et al. 2007), and our preliminary analyses of relatedness in free-living winter flocks (A. Liker, V. Bókony, Z. Tóth & A. Kulcsár, unpublished data) indicate that most sparrows have at least a few close relatives in their flocks. These facts suggest that sparrows have the opportunity to forage together with relatives. To test the effects of relatedness on foraging tactic use, we observed captive flocks in which sparrows could scrounge from differently related individuals. Specifically, we tested whether sparrows scrounge (1) at a different rate and (2) with different success from related and unrelated flockmates, as predicted by kin selection theory (see predictions 1 and 2 above). As the costs of scrounging are likely to differ between its two common forms typical for sparrows, aggressive and nonaggressive scrounging (Liker & Barta 2002), we analysed these behaviours separately. Furthermore, since individual characteristics such as dominance or sex may influence both strategy use (see above) and kin-biased behaviour (e.g. Burley et al. 1990), we also tested whether the effects of relatedness depend on these characteristics.

METHODS

Study Subjects

We captured house sparrows with mist nets between 15 June and 4 October 2005 in the Kittenberger Zoo in Veszprém, Hungary, where we have been studying the sparrow population since 2004. Most of the birds, 35 of the 44, were juveniles of the year. Because 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: from 44 birds, 19 were placed with one or more siblings and two with a parent in the captive flocks. Adults were caught either in September after cessation of reproduction or in June–July together with their offspring (and were held together in outdoor aviaries). We allocated the captured birds to two flocks (7 females and 14 males and 12 females and 11 males, respectively). Upon capture we measured body mass (±0.1 g), tarsus (±0.1 mm) and wing length (±1 mm), and took small blood samples (approximately 100 μl) for kinship analyses. Each individual was ringed with a numbered aluminium ring and three colour rings. We also marked the birds by painting small coloured signs with nontoxic paint (Deco painter, Marabu Co., Bietigheim-Bissengen, Germany) on their crown feathers to facilitate quick individual recognition during the observations.

Birds were held in two outdoor aviaries (5 × 4 m and 3 m high) ca. 5 m apart, with partial visual barriers (bushes) between them. Both aviaries contained roosting trees and small boxes for sleeping and resting. Water, sand and fine gravel (to facilitate digestion) were provided ad libitum and multivitamin droplets were regularly added to the water. Feeding took place on a grid (1.2 × 1.2 m) that contained 144 (12 × 12) equidistant wells (diameter 2.5 cm, depth 1.2 cm) for presenting food (Lendvai et al. 2004). We provided millet, oat, wheat and sunflower seeds ad libitum during a 4-week acclimatization period and between different observations. The birds apparently became familiar with the aviaries during acclimatization, and they had learned to use the grid by the time of the observations. Throughout the study we did not observe any aggression resulting in visible injuries, similarly to our previous studies on captive sparrow flocks (e.g. Lendvai et al. 2004, 2006). Birds maintained their weight in captivity (at the start of captivity: $\overline{X} \pm SE = 28.11 \pm 0.24$ g; at the end of captivity: 28.49 ± 0.22 g). After the observations we released all birds at the site of capture. To facilitate their survival after release, we provided bird food on feeders where we observed the released birds several times during winter. Some of them were recorded as breeding adults in the following spring.

Kinship Analyses

Blood samples were obtained from the brachial vein of captured birds and were stored in Queen's lysis buffer (Dawson et al. 1998) until analysis. DNA was extracted from the blood samples with a standard phenol–chloroform procedure, or with a Qiagen DNeasy Tissue Kit (Qiagen Inc., Valencia, CA, U.S.A.) following the producer's instructions. Seven highly polymorphic microsatellite loci were used for genotyping ($\overline{X} \pm SE = 11.86 \pm 0.74$ alleles per locus; see Appendix for details of allele sizes and frequencies). Primers for four dinucleotide loci (*Pdo1*, *Pdo2*: Neumann & Wetton 1996; *Pdo5*: Griffith et al. 1999; *Pdo8 mu*: GenBank: AF354422), one trinucleotide locus (*Pdo9*, AF354423) and one tetranucleotide locus (*Pdo3*, Neumann & 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 has been used successfully in genetic studies of sparrows (e.g. Jensen et al. 2003). In each primer pair, forward primers were fluorescently labelled on the 5′-end with HEX, JOE or FAM-6 dyes (Applied Biosystems Inc., Foster City, CA, U.S.A.). 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 analysed on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems Inc.) at the Biomi Ltd., Gödöllő, Hungary, using a ROX-labelled ILS-600 internal standard (Promega Corp., Madison, WI, U.S.A.). The data were analysed with the Genescan software (Applied Biosystems Inc.).

The ML-Relate computer program (Kalinowski et al. 2006) was used to calculate maximum likelihood estimates of relatedness (r) and relationship categories between individuals from genotypic data. This method accommodates null alleles during the relatedness estimations which had high frequencies at two loci (*Pdo2*: 0.20, *Pdo8*: 0.18; Appendix), and is considered to be more accurate than other estimators (Milligan 2003). We estimated allele frequencies, pairwise genetic relatedness and kinship categories by entering all individuals' genotypes into the program as if they were a single population, since no prior reference data were available about the studied sparrow population. We used ML-Relate to calculate the likelihood of four common relationships: U: unrelated; HS: halfsiblings; FS: full siblings, PO: parent–offspring (no other relationships are allowed by the software) and to determine relationships that had the highest likelihood for each pair of flockmates (Kalinowski et al. 2006). Flockmates with which a given individual had HS, FS and PO relationships were pooled and considered 'close kin' ($r = 0.30 \pm 0.02$; number of 'close kin' flockmates per individual $= 3.07 \pm 0.21$). The 'unrelated' flockmates were those birds with which a given individual was considered unrelated (U) according to ML-Relate ($r = 0.02 \pm 0.002$; number of 'unrelated' flockmates $= 17.95 \pm 0.27$). This categorization was likely to reflect real relationships with reasonable