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

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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.

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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

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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 ($\pm$0.1 g), tarsus ($\pm$0.1 mm) and wing length ($\pm$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

accuracy, because in our subsample of birds with known pedigree ($N = 121$ dyads, 26.1% of all dyads), 94.1% and 98.1% of the assigned categories matched the real (pedigree-based) relationships in the 'close kin' and the 'unrelated' group, respectively.

Collecting Behavioural Data

We observed the birds' foraging tactic use during six trials in flock 1 (duration per trial: $\overline{X} \pm SE = 5.7 \pm 0.17$ min; 34.4 min in total) and five trials in flock 2 (duration per trial: 7.5 ± 1.8 min; 37.5 min in total), after 2 h of food deprivation in the morning on 24 November (flock 1) and 20 December 2005 (flock 2). At the start of each trial, millet seeds were placed in 22 randomly chosen wells on the grid (ca. 120 seeds per well). After the provision of food, we started to record the behaviour of the birds with two synchronized digital video cameras. One video camera was fixed on a pole and filmed the whole grid, while the other camera was controlled by the observer through a one-way window ca. 2 m from the grid to take close-up pictures of the birds on the grid so that their individual markings were unambiguously recognizable. Because the cameras were synchronized and the wells were numbered, we could use close-up recordings to identify individuals on the other (whole-grid) records. Feeding trials lasted until all seed clumps were depleted and the birds left the grid.

We followed each bird throughout each trial on the whole-grid video record to analyse their behaviour (which tactics they used and with which flockmates) as follows. Feeding events were divided into two types, finding and joining. These terms were used instead of producing and scrounging, respectively, because we recorded actual feeding events and not directly observed tactic use, that is, whether a bird was searching as a producer or a scrounger (Mottley & Giraldeau 2000; Coolen et al. 2001). In finding events a bird discovered an unoccupied well and fed from it. In joining events the well from which the focal bird began to feed was already occupied by a feeding flockmate when the focal individual arrived. We further distinguished two types of joining: aggressive (AJ) and nonaggressive (NJ). Joining was considered aggressive when the focal individual attacked the well-owner before feeding from that well, while nonaggressive joining started without attacking. For each feeding event we also recorded the number of pecks per well (as a proxy for food intake) and the time spent at the well (± 0.5 s). From the latter we also calculated 'time feeding together' for each focal bird as the amount of time the owner and scrounger individuals spent foraging together at the same well (± 0.5 s) following an NJ event.

Data Processing and Statistical Analyses

We analysed the foraging behaviour of the birds by comparing their joining tactic use (AJ and NJ) against the two kinship groups: 'close kin' and 'unrelated' flockmates. Because three individuals had no 'close kin' flockmate, we analysed 41 birds' joining behaviour (582 joining events in total).

Behaviours (number of AJs and NJs, number of pecks during AJs and NJs, time feeding together) performed with the respective kinship groups were quantified as the total amount of behaviour performed by a focal bird with all members of a kinship group, divided by the number of individuals in that kinship group. We applied Box–Cox transformation (Box & Cox 1964) to all variables to improve their fit to a normal distribution (number of AJs: $\lambda_1 = -0.01$, $\lambda_2 = 0.02$; number of NJs: $\lambda_1 = 0.26$, $\lambda_2 = 0.03$; number of pecks during AJs: $\lambda_1 = -0.12$, $\lambda_2 = 0.3$; number of pecks during NJs: $\lambda_1 = 0.02$, $\lambda_2 = 0.3$; time feeding together: $\lambda_1 = -0.01$, $\lambda_2 = 0.08$). Statistical analyses were performed with R (R Development Core Team 2005). We used linear mixed-effect models (LME; 'lme' function of the 'nlme' R package; Pinheiro & Bates 2000) to assess the effects of kinship (as a fixed factor in

accordance with the kinship groups defined above) and other explanatory variables (see below) on the behaviour of birds. In LME models, parameter estimation is unaffected by an unbalanced design (Pinheiro & Bates 2000) such as the different numbers of individuals in our kinship groups. We included individual identity ('id') and flock identity ('flock') as two-level nested random factors ('id' nested in 'flock') in the models to control for potential pseudoreplication (e.g. Taillon & Côté 2007), because this random factor design is equivalent to repeated measures models in R (Pinheiro & Bates 2000; Faraway 2006). To investigate their potential effects, we also included the sex of the examined bird ('sex' henceforth) as a fixed factor and dominance rank as a covariate in the full models. Dominance ranks in the two flocks were calculated by de Vries's (1998) 'I and IS' algorithm from the outcomes of 788 (flock 1) and 542 (flock 2) aggressive interactions observed prior to the video recordings. We used restricted maximum likelihood methods for model estimation and F values to define the significance of the tested fixed effects ('anova.lme' function). We used a stepwise backward elimination procedure to choose the best model, starting with all main effects and their interactions with kinship, and dropping the predictor with the highest P value in each step, retaining only $P \leq 0.05$ effects in the final models (Grafen & Hails 2002). To balance type I and II errors, we relied on effect sizes instead of Bonferroni correction for significance levels, because the latter has been criticized in the field of behavioural ecology (Nakagawa 2004; Garamszegi 2006). To express effect size as the proportion of variance explained by each trait, we report the partial η^2 and its 95% confidence interval (Cohen 1988). All tests were two tailed with a 5% significance level.

RESULTS

Birds used AJ more often with unrelated flockmates than with close kin, and they also obtained significantly more food by AJ from unrelated birds than from close kin (Table 1, Fig. 1a,b). Furthermore, dominance rank was also significantly related to the frequency and success of AJ (Table 1).

During NJs, males tended to target their close kin less frequently than their unrelated flockmates, whereas females showed the opposite trend (Table 1, Fig. 2a). This kinship*sex interaction was also significant for the amount of food obtained by NJ: males tended to acquire fewer seeds from close kin than from unrelated birds but we found a reverse tendency for females (Table 1, Fig. 2b). Furthermore, more dominant birds took fewer seeds from their close kin by NJ than more subordinate birds, whereas the amount of food obtained from unrelated flockmates was not related to dominance rank (Table 1, Fig. 2c). The sexes did not differ in their dominance ranks ($F_{1,38} = 0.47$, $P = 0.498$).

Finally, sparrows spent significantly less time feeding together when they joined their close kin than when they joined unrelated flockmates by NJs (Table 1), and a significant interaction indicated that this kinship effect was mainly due to the behaviour of males but not females (Table 1, Fig. 2d).

DISCUSSION

In this study we investigated how relatedness between flockmates affects the use of aggressive and nonaggressive scrounging tactics in house sparrows, and found that kinship affected all studied behaviours associated with scrounging. First, we found that birds scrounged less often and scrounged less food by aggressive joining from their close relatives than from nonkin. Second, we found sex-dependent effects of relatedness on the use of the nonaggressive joining tactic: males always avoided their kin whereas females either showed the opposite tendencies (number and success of joinings) or did not appear to discriminate with

Table 1
Final LME models of aggressive (AJ) and nonaggressive joining (NJ), comparing behaviours performed with close kin and unrelated flockmates

Dependent variables	Predictors	df	F	η² (confidence interval)	P
Number of AJ	Dominance rank	1,38	4.70	0.11 (0–0.30)	0.037
	Kinship	1,40	9.16	0.18 (0.02–0.38)	0.004
Food obtained by AJ	Dominance rank	1,38	7.26	0.16 (0.01–0.36)	0.010
	Kinship	1,40	11.97	0.23 (0.04–0.42)	0.001
Number of NJ	Sex	1,38	2.00	0.05 (0–0.22)	0.166
	Kinship	1,39	0.36	0.01 (0–0.14)	0.552
	Kinship*sex	1,39	4.22	0.10 (0–0.29)	0.047
Food obtained by NJ	Dominance rank	1,37	1.60	0.04 (0–0.21)	0.214
	Sex	1,37	7.25	0.16 (0.01–0.36)	0.011
	Kinship	1,38	0.71	0.02 (0–0.16)	0.404
	Kinship*dominance rank	1,38	4.85	0.11 (0–0.31)	0.034
	Kinship*sex	1,38	6.90	0.15 (0.01–0.35)	0.012
Time feeding together during NJ	Sex	1,38	2.58	0.06 (0–0.24)	0.116
	Kinship	1,39	10.97	0.22 (0.03–0.41)	0.002
	Kinship*sex	1,39	4.25	0.10 (0–0.29)	0.046

respect to relatedness (time feeding together). Third, more dominant birds scrounged less food by nonaggressive joining from their close kin but not from unrelated flockmates. The avoidance of kin exploitation, especially by males and dominants, is in accordance with kin selection when the costs of scrounging are high for the

Figure 1. (a) Frequency of, and (b) number of feeding pecks during, aggressive joinings (AJ) with close kin and unrelated flockmates (*N* = 41). Means are shown ± SE. Dependent variables are plotted as residuals from the final linear mixed-effect models containing dominance rank as a significant predictor variable. Close kin and unrelated birds are flockmates estimated to be related (full and half sibs and parent–offspring) or unrelated, respectively, by the maximum likelihood method.
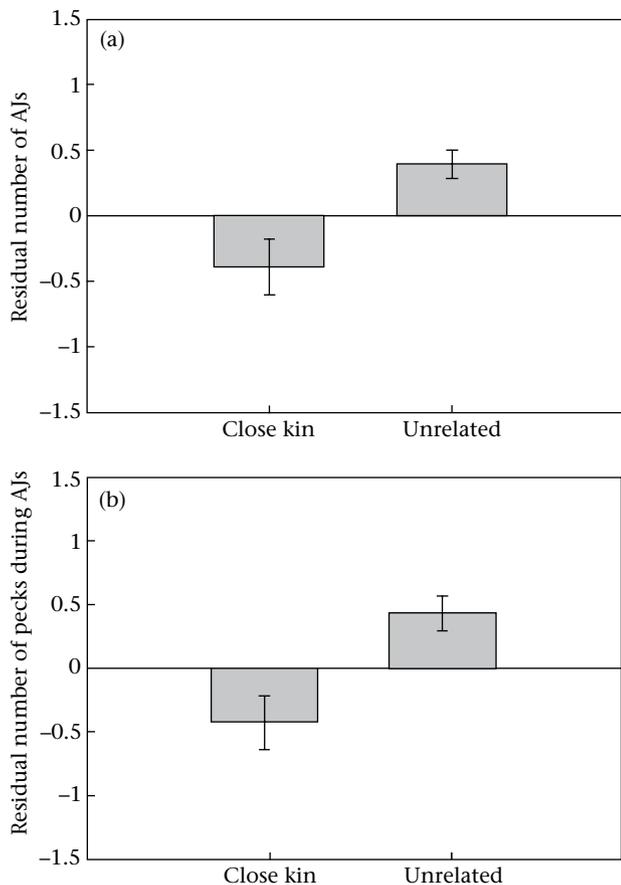
exploited birds. Our results suggest that house sparrows may take kinship into account during social foraging in a complex manner, adjusting their kin-exploiting behaviours to factors such as the potential cost to the target bird and their own sex and social status. We discuss these findings in detail below.

Since fighting may well be costly in terms of energy and the risk of injury, aggressive joining is likely to incur greater cost for exploited producers than nonaggressive joining. We found that sparrows used aggressive joining less often and so took less food from their close kin than from unrelated flockmates, irrespective of their sex and rank. This result implies that when it comes to the more costly form of exploitation, sparrows spare their close kin, in accordance with the predictions of kin selection theory. The higher cost of aggressive joining and the adaptive value of avoiding that tactic with closely related individuals are also indicated by previous findings on northwestern crows, where birds tended to scrounge nonaggressively rather than aggressively from their kin (Ha et al. 2003).
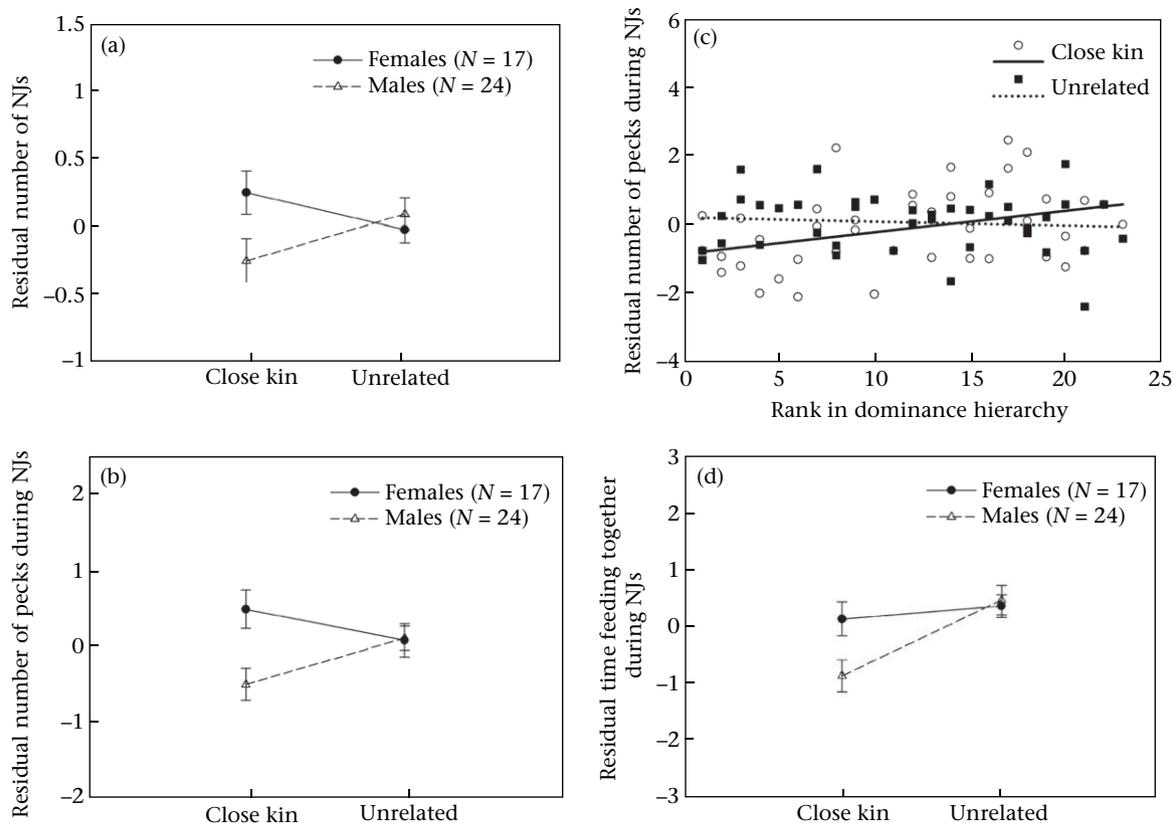
During nonaggressive joinings, males tended to avoid relatives, similarly to aggressive joinings, while females did not show clear discrimination: they either showed the opposite tendency or no difference in behaviours associated with nonaggressive joinings with close kin and unrelated birds. Currently we have no clear explanation for this sex difference. A factor that may contribute to it may be the sex-biased philopatric behaviour of the species. In house sparrows, typically the females disperse over greater distances (Anderson 2006), so they might be less likely to encounter close relatives in natural flocks than males. Thus, there may be weaker selection in females than in males to take relatedness into account during exploitive actions, and this may be especially relevant for less costly forms of exploitation such as nonaggressive joinings. On the other hand, males might be selected to avoid their close relatives during both types of scrounging, to spare their close kin's food-finding efforts.

In a hierarchically structured society, dominance rank may also modify the payoffs of any altruistic behaviour. For instance, the costs of kin helping may vary across individuals as their access to resources or actual physical condition also differs. For subordinates and individuals with low reserves, being helpful to relatives may be too costly because any altruistic act would directly jeopardize their own fitness, whereas dominants may better afford helping their kin. In accordance with this notion, we found that the more dominant the birds were the less food they scrounged from their close kin by nonaggressive joining, whereas dominants and subordinates obtained equal amounts of food from unrelated flockmates by this tactic. Although Lendvai et al. (2006) found that dominants and subordinates differ in their use of the joining tactic, it is unclear from our data why this dominance effect was detectable only for feeding rates during nonaggressive joinings and not for other behaviours and aggressive joinings. Owing to this lack of consistency, we suggest that further tests would be needed for a robust support or rejection of the possibility that dominant and subordinate individuals use scrounging differently to exploit their relatives.

Finally, our results also suggest the presence of kin recognition mechanisms in house sparrows. Although the capability of kin discrimination is well known in several bird species and current evidence suggests that associative learning is the most likely mechanism of kin discrimination in avian societies (Blaustein et al. 1987; Komdeur & Hatchwell 1999; Sharp et al. 2005), there has been no experimental evidence in house sparrows specifically. Since we found differences between several aspects of scrounging behaviour towards close kin and nonkin birds, sparrows are likely to be able to distinguish between genetically closely related and unrelated flockmates. As the close kin group in our study included mostly siblings and parents, further research is needed to clarify

Figure 2. Behaviours ($\overline{X} \pm$ SE) associated with nonaggressive joinings (NJ) with close kin and unrelated flockmates. Dependent variables are plotted as residuals from the final linear mixed-effect models without the examined interaction and its main effects. (a) Number of NJs, (b) number of feeding pecks during NJs by males and females, (c) number of feeding pecks during NJs with close kin and unrelated individuals in relation to rank, and (d) time feeding together with close kin and unrelated individuals. In (c), dominance rank 1 refers to the most dominant flock member. Kinship groups are defined as in Fig. 1.

whether this discrimination ability is restricted mostly/exclusively to individuals familiar from the early life period or whether sparrows can recognize unfamiliar kin, too.

In conclusion, our results suggest that kinship affects the use of social-foraging tactics that exploit flockmates in house sparrows. Such support for the kin selection theory is interesting given that most cases of kin-favouring behaviours have been found in species that live in kin groups (Sklepkovych 1997; Pravosudova et al. 2001). Our study adds to the scarce existing evidence that kin-biased social behaviour occurs even in species that neither breed cooperatively nor form permanent family groups.

Acknowledgments

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APPENDIX

Table A1
Number of alleles, allele sizes and their estimated frequencies in the seven highly polymorphic microsatellite loci for 44 house sparrows in this study

	Pdo1	Pdo2	Pdo3	Pdo5	Pdo8 mu	Pdo9	Mcyu4
Number of alleles	12	14	13	13	12	8	11
Allele sizes (frequencies)	154 (0.136)	169 (0.023)	113 (0.023)	203 (0.114)	195 (0.143)	375 (0.193)	179 (0.159)
	172 (0.023)	171 (0.023)	117 (0.011)	233 (0.011)	197 (0.046)	378 (0.375)	181 (0.102)
	174 (0.261)	179 (0.012)	121 (0.023)	237 (0.034)	199 (0.203)	384 (0.057)	183 (0.114)
	180 (0.011)	183 (0.146)	125 (0.080)	239 (0.034)	201 (0.064)	387 (0.034)	187 (0.068)
	184 (0.091)	185 (0.023)	129 (0.193)	241 (0.011)	208 (0.046)	390 (0.148)	189 (0.080)
	186 (0.057)	187 (0.218)	133 (0.171)	243 (0.102)	210 (0.144)	405 (0.011)	191 (0.080)
	188 (0.136)	189 (0.136)	137 (0.125)	245 (0.114)	212 (0.035)	409 (0.171)	193 (0.057)
	192 (0.136)	191 (0.100)	141 (0.171)	247 (0.330)	216 (0.023)	414 (0.011)	195 (0.091)
	196 (0.046)	193 (0.011)	146 (0.080)	249 (0.057)	218 (0.011)		197 (0.034)
	198 (0.034)	195 (0.046)	150 (0.080)	251 (0.114)	224 (0.034)		199 (0.171)
	200 (0.023)	201 (0.011)	154 (0.023)	253 (0.057)	226 (0.057)		201 (0.046)
	208 (0.046)	203 (0.012)	159 (0.011)	255 (0.011)	228 (0.011)		
		205 (0.011)	163 (0.011)	259 (0.011)	NULL (0.184)		
		207 (0.023)					
		NULL (0.203)					