

Kinship and aggression: do house sparrows spare their relatives?

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Abstract Kin-selection theory predicts that relatedness may reduce the level of aggression among competing group members, leading to indirect fitness benefits for kin-favoring individuals. To test this hypothesis, we investigated whether relatedness affects aggressive behavior during social activities in captive house sparrow (*Passer domesticus*) flocks. We found that sparrows did not reduce their aggression towards kin, as neither the frequency nor the intensity of fights differed between close kin and unrelated flock-mates. Fighting success was also unrelated to kinship and the presence of relatives in the flock did not influence the birds' dominance rank. These results suggest that the pay-offs of reduced aggression towards kin may be

low in non-breeding flocks of sparrows, e.g. due to competition among relatives as predicted by a recent refinement of kin-selection theory. Our findings indicate that the significance of kin selection may be restricted in some social systems such as winter aggregations of birds.

Keywords Genetic relatedness · Aggression · Dominance · Kin discrimination · House sparrow

Introduction

Living in groups has several drawbacks that may reduce its benefits such as increased foraging efficiency or more effective anti-predator behaviors (Alexander 1974; Krause and Ruxton 2002). One of these costs is the intense competition among group members, often leading to asymmetric distribution of benefits, e.g. when dominant individuals can gain increased or exclusive access to resources (Vehrencamp 1983). However, kin-selection theory (Hamilton 1964) predicts that individuals may gain indirect fitness benefits through reduced aggression toward kin by decreasing their relatives' costs of fighting and/or by contributing to their kin's access to limited resources. In accordance with this theory, reduced conflicts with relatives have been found in several vertebrate species, including birds (e.g. Butovskaya 1993; Sklepkovych 1997, Ensminger and Meikle 2005). For example, in many experimental studies reduced aggression against relatives was interpreted as evidence for kin recognition (e.g. Holmes 1986; Walls and Roudebush 1991). Nevertheless, evidence for indirect fitness effects of such behaviors in birds is scarce, for instance because most studied cases of reduced aggression towards kin can be interpreted as a form of prolonged parental care, i.e. adults are more aggressive

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towards unrelated juveniles than towards own young (Ekman et al. 1994; Hatch and Lefebvre 1997; Pravosudova et al. 2001).

In this study we investigated the effects of kinship on aggression in a simple social system, the winter flocks of house sparrows (*Passer domesticus*). Sparrows form flocks during the non-breeding season that consist of ten to 30 or more individuals and flock-members perform various activities together such as foraging, roosting, and dust-bathing (Anderson 2006). In the flocks birds form social hierarchy and gain social status through aggressive interactions, competing frequently for resources with each other, particularly for food and roosting sites (e.g. Møller 1987; Liker and Barta 2001). No permanent family groups have been observed in this species, thus any fitness benefit of kin-helping behavior in the non-reproductive period is likely to be indirect. Our preliminary analyses of relatedness in free-living winter flocks (A. Liker, V. Bókony, A. Kulcsár, Z. Tóth, K. Szabó, B. Kaholek, and Zs. Péntes, unpublished data) and 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, so birds have the opportunity to behave differently toward relatives and unrelated flock-mates. Accordingly, we found in captive flocks that birds used the aggressive form of scrounging less often against and obtained less food by that tactic from their close kin than from unrelated birds during social foraging (Tóth et al. 2009).

To test the effects of relatedness on agonistic interactions, we observed captive flocks in which sparrows could interact with differently related individuals. Specifically, (1) we tested whether sparrows initiate less attacks against, participate in contests at a lower rate with, or show reduced fighting intensity against kin compared to unrelated flock-mates, according to the predictions of kin-selection theory. (2) We examined whether sparrows achieve different fighting success against kin and non-kin flock-mates. (3) We also tested whether the presence of relatives influenced the achieved rank in dominance hierarchy. Throughout the study, we applied two alternative criteria to distinguish

between kin and non-kin companions, because both the degree of relatedness and familiarity from the early developmental period may influence kin-biased behaviors. Thus, we examined whether sparrows differently contest (1) their close kin or (2) their same-brood siblings as compared to other flock-mates.

Materials and methods

Study subjects

We captured house sparrows with mist nets in 2005–2006 in the Kittenberger Zoo in Veszprém (Hungary), where we have been studying the sparrow population since 2004. 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. 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). Sex ratio of the flocks (Table 1) was similar to those of free-living foraging flocks at our study site (41–63%, calculated from ringing data [A. Liker, V. Bókony, A. Kulcsár, Z. Tóth, unpublished data]; see also Bókony et al. 2008) and those reported by Breitwisch and Hudak (1989). 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), so dependent young's lives were not risked by our work. Upon capture we measured body mass (± 0.1 g) and took small blood samples (approximately 100 μ l) for kinship analyses. Each individual was ringed with a numbered metal ring and three color rings. We also marked the captive birds by painting small colored signs (using Deco painter, Marabu, Germany) on their crown feathers to facilitate quick individual recognition during the observations.

Birds were held in outdoor aviaries (approximately 5 (W) \times 4(L) \times 3(H) m). In 2005 flock 1 and 2 were held

Table 1 Characteristics of the captive house sparrow flocks

	Flock 1	Flock 2	Flock 3
Study period	2005 October–November	2005 October–December	2006 October–December
Number of individuals	23	21	17
Males	11	14	10
Females	12	7	7
Number of same-brood siblings	10 (3 dyads, 1 tetrad)	9 (3 dyads, 1 triad)	10 (5 dyads)
Number of observed agonistic interactions			
Flock total	788	542	766
Per individual (mean \pm SE)	34.26 \pm 5.56	25.81 \pm 3.95	45.06 \pm 6.89

separately in two aviaries ca. 5 m apart, with partial visual barriers (bushes) between them. 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. We supplied millet, oat, wheat, and sunflower seeds ad libitum for food during a 4-weeks long acclimatization period and during observations. Throughout the study, we did not observe severe aggression resulting in visible injuries, similarly to our previous studies on captive sparrow flocks (e.g. Lendvai et al. 2004, 2006). Birds did not lose weight in captivity, their weight even increased slightly during the study (at the start of captivity [mean \pm SE]: 27.85 \pm 0.19 g; at the end of captivity: 28.23 \pm 0.19 g; paired *t* test: $t_{60}=-2.93$, $P=0.005$). 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 also recorded as breeding adults in the following spring.

Kinship analyses

Blood samples were obtained from the brachial vein of captured birds, as a standard for blood-taking from 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 (13.29 \pm 0.78 alleles per locus; see electronic "Appendix" for details about allele sizes and frequencies). 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, Budapest, Hungary) forward primers were fluorescently labeled on the 5'-end with HEX, JOE or FAM-6 dyes (Applied Biosystems). PCR reactions consisted of approximately 100 ng of template DNA, 0.5 μ M of each primer, 0.2 mM dNTPs, 2 mM MgCl₂, 1 unit of Taq DNA polymerase (Fermentas, Vilnius, Lithuania) and the 10 \times Taq buffer in a final volume of 25 μ l. To resolve alleles, all amplified PCR products were analyzed on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems) at the Biomi (Gödöllő, Hungary) using ROX-labeled ILS-600 internal standard (Promega, Madison, WI,

USA). Allele sizes were determined by using the GeneScan software (Applied Biosystems).

ML-Relate computer program (Kalinowski et al. 2006) was used to calculate maximum likelihood estimates of pair-wise relatedness and relationship categories between individuals (see below) from genotypic data. This method accommodates null alleles that had high frequency at two loci (*Pdo2*: 0.20, *Pdo8*: 0.18) and is considered to be more accurate than other estimators (Milligan 2003). Allele frequencies, pair-wise genetic relatedness, and kinship category estimations were performed by entering all individuals' genotype in the software as of a single population, since no prior genetic reference data was available for the studied sparrow population.

Collecting behavioral data

Behavioral observations took place between 8:00 and 17:00 hours, in randomly distributed 1-h long periods. Through a one-way window, we recorded all agonistic interactions among feeding, drinking, dust-bathing, and roosting birds. The identity of individuals involved in dyadic fights was recorded as well as the initiator and the winner of the contests (Liker and Barta 2001, Bókonyi et al. 2006). We scored the intensity of aggression for the observed interactions using the following categories: 1—supplant: intentional movement without physical contact; 2—threat: wing display or beak gaping without physical contact; 3—peck: short physical contact; 4—fight: prolonged physical contact (for similar approaches, see Jawor 2000 and Hein et al. 2003). We computed each bird's fighting success against each flock-mate as the number of wins divided by the total number of aggressive interactions by that dyad. From the outcomes of all repeated aggressive interactions we calculated within-flock dominance rank for each bird by de Vries' (1998) "I and IS" algorithm. The rank indicates the bird's position in the hierarchy, i.e. rank 1 has been assigned to the most dominant bird and higher numerical values to less dominant individuals.

Data processing and statistical analyses

We analyzed the aggressive interactions of the birds in two ways, in which we distinguished different kinship groups. In Analysis 1, we separated 'close kin' and 'unrelated' kinship groups. To do so, we used ML-Relate to calculate the likelihood of four common relationships: U—unrelated, HS—half-siblings, FS—full-siblings, PO—parent—offspring (no other relationships are allowed in the software) and to determine relationship that had the highest likelihood for each pair of flock-mates (Kalinowski et al. 2006). Flock-mates with which a given individual had HS, FS, and PO relationships were pooled and considered as 'close kin'

(Table 2). The ‘unrelated’ flock-mates were those birds with which a given individual was assigned being unrelated (U) according to ML-Relate (Table 2). This categorization is likely to reflect real relationships with reasonable accuracy, because in our subsample of birds with known pedigree ($N=257$ dyads, 42.9 % of all dyads), 90.0% and 96.9% of the assigned categories matched the pedigree-based relationships in the ‘close kin’ and the ‘unrelated’ group, respectively. Three individuals had no ‘close kin’ flock-mate, so these individuals were excluded from the analysis.

In Analysis 2, we focused on those juveniles that were known to have same-brood siblings as flock-mates according to our pedigree data. For these birds we distinguished three types of flock-mates based on differences in genetic relatedness and early familiarity (Table 2): (1) ‘sibling’ flock-mates, i.e. closely related individuals from the same brood; (2) ‘non-sib close kin’, i.e. all close kin flock-mates according to the category estimation of ML-Relate, without being familiar from nestling period, which means that neither parents nor same-brood siblings were present in this kinship group; (3) ‘unrelated’ flock-mates, i.e. birds with which a given individual was assigned being unrelated (U) according to ML-Relate. Relatedness coefficient was significantly different among these three kinship groups in both sexes (Kruskal–Wallis test, females: $\chi_2^2=12.80$, $P=0.002$; males: $\chi_2^2=29.04$, $P<0.001$). Eleven out of 29 siblings had no ‘non-sib close kin’ flock-mate and were excluded from the analysis.

In Analyses 1 and 2 we tested the possible effects of kinship on four variables associated with aggression. The number of attacks and the number of fights against the respective kinship groups were quantified as the total amount of behavior performed by a focal bird against all members of a kinship group, divided by the number of individuals in that kinship group. In relation to these two variables, we analyzed 58 birds’ data (2,044 agonistic encounters in sum) in Analysis 1 and 18 birds’ data (589 agonistic encounters in sum) in Analysis 2. The intensity of fights against a given kinship group was calculated as the average value of fighting intensities against the members of that kinship group. Due to missing data on intensity of some fights between focal birds and their kin, here we analyzed 57 birds’ data in Analysis 1 and 16 birds’ data in

Analysis 2. Fighting success against the respective kinship groups was quantified as the average fighting successes (proportion of wins) of the focal bird against the members of that kinship group. Due to missing data on success of some fights between focal birds and their kin, here we analyzed 56 birds’ data in Analysis 1 and 15 birds’ data in Analysis 2. In both Analysis 1 and 2, we applied Box–Cox transformation to the number of attacks and number of fights (in Analysis 1: number of attacks, $\lambda_1=0.26$, $\lambda_2=0.08$; number of fights, $\lambda_1=0.26$, $\lambda_2=0.2$; in Analysis 2: number of attacks, $\lambda_1=0.55$, $\lambda_2=0.09$; number of fights, $\lambda_1=0.28$, $\lambda_2=0.2$) in order to improve their fit to normal distribution (Box and Cox 1964).

Statistical analyses were performed in the R computing environment (R Development Core Team 2005). We used linear mixed-effect models (‘lme’ function of the ‘nlme’ R package; Pinheiro and 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 behavior of birds. In LME models, parameter estimation is unaffected by unbalanced design (Pinheiro and Bates 2000) such as the different number of individuals in our kinship groups. In Analysis 1 we included individual identity (‘id’) and flock identity (‘flock’) as 2-level nested random factors (‘id’ nested in ‘flock’) in the models, while in Analysis 2 we applied 3-level random factor design with individual identity, brood identity (‘brood’), and flock identity (‘id’ nested in ‘brood’ nested in ‘flock’; note that we had no pedigree information for all individuals, so brood identity information could not be used in Analyses 1). These random factor designs are equivalent to repeated measures models in R (Pinheiro and Bates 2000; Faraway 2006), i.e. statistical comparisons are made within individuals, and by their applications we controlled for potential pseudoreplication (e.g. Taillon and Côte 2007). To control for potential confounding effect of sex, we also included sex of the focal bird (‘sex’ henceforth) as fixed factor into the full models. We used restricted maximum likelihood methods for model estimation and F values to define significance of the tested fixed effects (‘anova.lme’ function). We used stepwise backward elimination procedure to choose the best model, starting with both main effects (i.e. sex and kinship) and their interaction, and

Table 2 Pair-wise genetic relatedness and number of opponents per individual in each kinship group in the two analyses

Relatedness (r_{ML}) between individuals was estimated by maximum likelihood method

	Kinship groups	$r_{ML}(\text{mean} \pm \text{SE})$	No. of opponents (mean \pm SE)
Analysis 1 ($N = 58$)	Close kin	0.34 \pm 0.02	2.72 \pm 0.18
	Unrelated	0.02 \pm 0.002	16.83 \pm 0.31
Analysis 2 ($N = 18$)	Same-brood sibling	0.49 \pm 0.04	1.50 \pm 0.19
	Non-sib close kin	0.20 \pm 0.01	1.89 \pm 0.21
	Unrelated	0.02 \pm 0.004	16.78 \pm 0.43

dropping the predictor with the highest P value in each step, retaining only $P \leq 0.05$ effects (if there was any) in the final models (Grafen and Hails 2002).

Nonparametric statistical methods were applied to investigate the effect of kin individuals' presence on dominance rank: we used (1) Spearman correlations to test for associations between dominance rank and the number of close kin flock-mates (range, 0–6) and (2) Wilcoxon signed-rank tests to examine whether siblings achieve different rank in dominance hierarchy compared to birds without sib flock-mates. To balance Type I and II errors, we (1) estimated effect sizes for the LME models (see Nakagawa 2004; Garamszegi 2006) as the proportion of variance explained by each trait, i.e. η^2 and its 95% confidence interval (Cohen 1988) and (2) we applied sequential Bonferroni-correction for significance levels in the non-parametric analyses that were performed for the three flocks separately. All tests were two-tailed with a 5% significance level.

Results

The effect of kinship on aggressive behavior

In Analysis 1 (i.e. close kin versus unrelated birds), kinship between flock-mates had no significant effect on any aspect of aggressive behavior either by itself or in interaction with sex (Table 3). Similarly, in Analysis 2 (i.e. siblings versus non-sib close kin versus unrelated birds) kinship had no significant effect on aggressive behaviors either by itself or in interaction with sex (Table 4). In both Analyses, no effect of sex was found on any of the dependent variables (all $P > 0.117$ in Analysis 1; all $P > 0.098$ in Analysis 2).

The effect of kin's presence on dominance rank

The birds' dominance rank achieved in their flocks was not related to the number of close kin flock-mates (flock 1: $r_S = -0.129$, $P = 0.417$; flock 2: $r_S = 0.173$, $P = 0.287$; flock 3:

$r_S = 0.287$, $P = 0.099$). Similarly, the rank of birds with sibling flock-mates did not differ from others' (Wilcoxon signed-rank tests, flock 1: $W = 41$, $P = 0.134$; flock 2: $W = 71$, $P = 0.287$; flock 3: $W = 14$, $P = 0.043$; the result found in flock 3 is not significant after Bonferroni-correction).

Discussion

In this study we investigated how relatedness between flock-mates affects several aspects of aggressive behavior in non-breeding house sparrow flocks. In two sets of analyses we consistently found that sparrows did not mitigate their aggression towards relatives in any aspect of agonistic behaviors. Although sparing relatives during agonistic interactions might be a way to attain indirect fitness benefits according to kin-selection theory, sparrows do not appear to do so.

According to Hamilton's rule, kin-helping may only evolve if the benefit of the helped individual (b) multiplied by the relatedness between the two interacting individuals (r_{xy}) exceeds the cost of helping (c ; $r_{xy} \times b - c > 0$, Hamilton 1964). Thus our results may simply be explained by the low benefits to costs ratio of reduced aggression towards kin. Although sparrows do spare their close relatives in certain contexts such as aggressive scrounging (Tóth et al 2009), the pay-offs of kin-helping might vary across different social activities and environmental conditions. For example, attacking kin for getting a better dust-bathing site or a more sheltered resting place might incur less cost in terms of inclusive fitness than taking the kin's food away. If so, sparrows would not be selected to favor their kin during competition for less valuable resources or when defeat does not directly risk fitness. Furthermore, in our previous study on social foraging, food restrictions might have increased the benefits of helping (a small amount of food may be valuable for a hungry kin), whereas birds were fed ad libitum in this study. On the other hand, restrained aggression towards kin may be costly if the aggressive encounters are witnessed by other group members and the

Table 3 Aggression against close kin and unrelated flock-mates in Analysis 1

Dependent variables	Close kin ^a (mean \pm SE)	Unrelated ^b (mean \pm SE)	df	F value	η^2 [CI] ^c	P value
Number of attacks	2.11 \pm 0.27	1.82 \pm 0.19	1, 57	0.03	0.001 [0–0.02]	0.867
Number of fights	4.11 \pm 0.34	3.64 \pm 0.28	1, 57	1.87	0.03 [0–0.16]	0.177
Intensity of fights	1.91 \pm 0.05	1.98 \pm 0.03	1, 56	1.33	0.02 [0–0.14]	0.254
Fighting success	0.55 \pm 0.04	0.55 \pm 0.02	1, 55	0.06	0.001 [0–0.04]	0.815

Statistics are derived from LME models with individual identity and flock identity as random factors and kinship as fixed factor

^a Flock-mates estimated to be full or half sibs or parent–offspring dyad by maximum likelihood method

^b Flock-mates estimated to be unrelated by maximum likelihood method

^c Effect size (proportion of variance explained) and its 95% confidence interval

Table 4 Aggression against siblings, non-sib close kin, and unrelated flock-mates in Analysis 2

Dependent variables	Sibling ^a (mean ± SE)	Non-sib close kin ^b (mean ± SE)	Unrelated ^c (mean ± SE)	df	F value	η^2 [CI] ^d	P
Number of attacks	2.02 ± 0.38	1.65 ± 0.27	1.60 ± 0.23	2, 34	0.54	0.03 [0–0.16]	0.586
Number of fights	4.43 ± 0.61	3.28 ± 0.87	3.32 ± 0.41	2, 34	2.90	0.15 [0–0.33]	0.069
Intensity of fights	2.04 ± 0.13	1.84 ± 0.10	1.91 ± 0.07	2, 30	1.29	0.08 [0–0.26]	0.290
Fighting success	0.52 ± 0.09	0.53 ± 0.08	0.44 ± 0.05	2, 28	0.76	0.05 [0–0.22]	0.475

Statistics are derived from LME models with individual identity, brood identity, and flock identity as random factors and kinship as fixed factor

^a Flock-mates known to be same-brood siblings based on pedigree

^b Flock-mates estimated to be full or half sibs or parent–offspring dyad by maximum likelihood method, but not same-brood siblings

^c Flock-mates estimated to be unrelated by maximum likelihood method

^d Effect size (proportion of variance explained) and its 95% confidence interval

information about the fighting ability of the contestants is used by bystanders (Coulter et al. 1996). If such bystander effect (Dugatkin 2001) exists in house sparrows, potential benefits of reduced kin aggression may be overridden by the costs that kin-helping birds would suffer by demonstrating reduced fighting potential to other flock-mates.

An alternative explanation, not mutually exclusive with the previous one, may be provided by recent refinements of Hamilton's original theory (Taylor 1992a, 1992b; Queller 1994), suggesting that competition among relatives may reduce or even nullify the benefits of being altruistic toward relatives. Specifically, as the helper becomes more related to the competitors of the helped individual (r_{xe}) and/or the kin-favoring behavior escalates the general level of competition (d), the advantage of kin-helping in terms of indirect fitness diminishes ($r_{xy} \times b - c - r_{xe} \times d > 0$, West et al. 2002). Since the number of kin individuals was relatively high in the flocks (on average 15% of the birds' flock-mates were close kin), the value of r_{xe} might have also been high, contributing to the lack of a reduction in aggression towards kin. Due to the house sparrow's sedentary nature (Anderson 2006) such abundance of related flock-mates is also likely in wild flocks. For example, we found in free-living wintering flocks that on average 14% of an individual's flock-mates are close relatives (A. Liker, V. Bókony, A. Kulcsár, Z. Tóth, K. Szabó, B. Kaholek, and Zs. Péntzes, unpublished data). Therefore, competition among kin may have a similar effect in natural flocks.

Our results also consistently showed that kinship had no effect on the sparrows' fighting success in any context. Furthermore, neither the number of close kin nor the presence of siblings in the flock influenced the birds' dominance rank, suggesting that relatives do not help each other to achieve higher rank in the hierarchy. Social support by kin group-mates during agonistic interactions can be advantageous because it may increase social status and facilitate access to resources, as it has been found in several primates (reviewed in Chapais 1992) and also in some bird

species (e.g. Black and Owen 1989; Weiss and Kotrschal 2004). However, supportive behavior is often confined to either parent–offspring dyads or older–younger siblings, when the supporter is dominant to the beneficiary's all contestants, thus is able to intervene successfully during the agonistic interactions of its kin. Since most sparrows were first-year juveniles in our study, the general absence of kin supporting might have been simply due to that potential supporters did not achieve adequate rank in the hierarchy to help their kin. However, the low incidence of known parent–offspring dyads in our captive flocks (1.3%) was similar to that we found in free-living flocks (0.4%; A. Liker, V. Bókony, A. Kulcsár, Z. Tóth, K. Szabó, B. Kaholek and Zs. Péntzes, unpublished data).

Sexes may differ in their behavior towards kin, for example, male house sparrows tend to avoid exploiting their close kin by non-aggressive scrounging whereas females do not (Tóth et al. 2009). However, we did not find any sex difference in this study in various aggressive behaviors toward kin. This may be related to the fact that males and females were not different either in their overall aggressiveness or dominance, which is consistent with the findings of several previous studies (Jawor 2000; Liker and Barta 2001; Tóth et al. 2009).

The consistent lack of kinship-effects on sparrows' aggression raises the question whether these birds are able to recognize their kin at all. Kin recognition is well known in several birds, but usually related to social association during early lifetime instead of the presence of real (i.e. genetically based) kin-discriminating mechanisms (Komdeur and Hatchwell 1999; Komdeur et al. 2004; Sharp et al. 2005). So far, no experiment has been carried out to investigate kin recognition per se in house sparrows; however, recent studies show that sparrows behave differently toward their kin in some contexts. We previously found that sparrows exploit their close kin and non-kin flock-mates differently by scrounging during social foraging (Tóth et al. 2009), although the close-kin group in that

study included mostly siblings and parents. We also observed a preference among captive sparrows to follow their siblings during various social activities (Z. Tóth, V. Bókony, Á.Z. Lendvai, K. Szabó, Zs. Péntzes, and A. Liker, unpublished data). These results suggest that sparrows are able to discriminate between kin and unrelated individuals, at least when kin is familiar from the nestling period. Further research is needed to clarify whether sparrows are able to recognize non-familiar relatives.

Overall, our findings suggest that the general pay-offs of reduced aggression towards kin might be low in wintering house sparrow flocks. These results indicate that in animal societies that are not characterized by aggregation of close kin, such as winter flocks of birds, kin selection may have little influence on some forms of social behavior.

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Ethical standards Our study complied with the current laws of Hungary, and the permission was provided by the Balaton Uplands National Park (permission number: 9135-2/2004).

Conflict of interest The authors declare that they have no conflict of interest.

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