

Fine-scale kin recognition in the absence of social familiarity in the Siberian jay, a monogamous bird species

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Abstract

Kin recognition is a critical element to kin cooperation, and in vertebrates, it is primarily based on associative learning. Recognition of socially unfamiliar kin occurs rarely, and it is reported only in vertebrate species where promiscuity prevents recognition of first-order relatives. However, it is unknown whether the recognition of socially unfamiliar kin can evolve in monogamous species. Here, we investigate whether genetic relatedness modulates aggression among group members in Siberian jays (*Perisoreus infaustus*). This bird species is genetically and socially monogamous and lives in groups that are formed through the retention of offspring beyond independence, and the immigration of socially unfamiliar nonbreeders. Observations on feeders showed that genetic relatedness modulated aggression of breeders towards immigrants in a graded manner, in that they chased most intensely the immigrant group members that were genetically the least related. However, cross-fostering experiments showed that breeders were equally tolerant towards their own and cross-fostered young swapped as nestlings. Thus, breeders seem to use different mechanisms to recognize socially unfamiliar individuals and own offspring. As Siberian jays show a high degree of nepotism during foraging and predator encounters, inclusive fitness benefits may play a role for the evolution of fine-scale kin recognition. More generally, our results suggest that fine-graded kin recognition can evolve independently of social familiarity, highlighting the evolutionary importance of kin recognition for social species.

Keywords: aggression, cooperation, paternity, self-referent phenotype matching, social evolution, social familiarity

Received 8 August 2014; revision received 1 October 2015; accepted 8 October 2015

Introduction

Genetic relatedness among individuals is an important factor modulating their social life. Related individuals may form cooperative societies, as is the case in eusocial insects or cooperatively breeding mammals and birds (Clutton-Brock 2002). A key adaptation that facilitates kin-based cooperation is kin recognition because fitness benefits resulting from cooperation depend on the relatedness between individuals (Hamilton 1964). In

cooperatively breeding animals, helpers preferentially assist close relatives (Komdeur & Hatchwell 1999). Accordingly, a higher degree of kin discrimination is found in cooperatively breeding bird species where the average relatedness among group members is low due to extra-pair paternity, or in species where helping at the nest provides a greater fitness benefit (Cornwallis *et al.* 2009).

A direct way of recognizing kin is through recognition alleles (Hamilton 1964; Crozier 1987), which have been found in a few social invertebrates (Keller & Ross 1998) and micro-organisms (Queller *et al.* 2003). In vertebrates, kin are mostly recognized based on associative

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learning through social familiarity (Komdeur & Hatchwell 1999; Sharp *et al.* 2005). Recognition of socially unfamiliar kin only is known in species where promiscuity prevents recognition of siblings (Petrie *et al.* 1999; Mateo & Johnston 2000; Hain & Neff 2006), which can recognize kin through self-referent phenotype matching (Hauber & Sherman 2001). Yet, kin recognition of unfamiliar individuals may be widespread. Birds preferably mate with less related individuals to reduce the costs that can arise from inbreeding (Arct *et al.* 2015; but see Lehtonen & Kokko 2015), and humans are more likely friends with individuals that have similar genotypes (Christakis & Fowler 2014).

Social interactions between individuals are not only cooperative but also agonistic, and individuals display aggression or cannibalism preferentially towards unrelated individuals (Waldman 1988; Pfennig *et al.* 1993). Kin recognition can reduce the costs that arise from competing with related individuals, yet to date no study looked into the influence of fine-scale differences in kinship on agonistic behaviours. Thus, it remains unknown whether recognition of socially unfamiliar kin can occur in a competitive context and whether this could extend beyond the recognition of first-order relatives.

Here, we look at the influence of genetic relatedness on aggressive interactions in the absence of social kin recognition cues in a group-living bird species, the Siberian jay (*Perisoreus infaustus*). Breeders form long-term bonds and are socially and genetically monogamous (Ekman *et al.* 1994; Gienapp & Merila 2010). Groups can contain up to seven members and are formed through the retention of the breeders' own offspring from different cohorts for up to 5 years (hereafter termed retained offspring), and/or the immigration of unrelated individuals (hereafter termed immigrants; Ekman *et al.* 1994). Within broods, socially dominant juveniles expel their subordinate siblings 6–8 weeks after fledging (Ekman *et al.* 2002). The expelled juveniles are forced to leave the parental territory and join another group, usually more than four territories away from the natal territory (Griesser *et al.* 2008, 2014).

As a result of the dispersal pattern, relatedness within Siberian jay groups is variable and has a bimodal distribution. It includes first-order relatives (breeders-offspring) and immigrants whose relatedness with respect to the other group members varies. The dichotomy in relatedness within groups (family members vs. immigrants) affects the social interactions between individuals. Breeders give retained offspring preferential access to resources (Ekman *et al.* 1994) and antipredator protection (Griesser 2003, 2009; Griesser & Ekman 2004, 2005), but withhold these benefits from immigrants and frequently displace and chase them (Ekman *et al.* 1994). Thus, our study system allows an investigation of the

influence of genetic relatedness on social interaction between group members.

In many group-living species, aggression among group members is linked to reproductive opportunities and dominant individuals specifically display aggression towards group members that threaten their dominance status (Kutsukake & Clutton-Brock 2006). In Siberian jays, only the breeding pair is reproductively active, and thus, nonbreeders can gain fitness only by becoming breeder (Ekman *et al.* 1994). Earlier studies showed that most aggression is exhibited by breeders that in particular display aggression towards same-sex immigrants (Ekman & Sklepkovych 1994), thereby limiting their access to food (Griesser 2003). Immigrants can seek conflicts with breeders during the breeding season, and thus, the presence of immigrants is associated with a lower nestling body condition (Griesser *et al.* 2008).

We investigated whether genetic relatedness modulates aggressive interactions between Siberian jay group members foraging at feeders. To assess whether breeders are socially unfamiliar with immigrants before their settlement, we used data on between-group encounters and dispersal distances. An earlier study showed that retained offspring reduce the chances of immigrants settling in their group (Griesser *et al.* 2008), but it is unknown whether differences in genetic relatedness between breeders and immigrants influence settlement decisions. Thus, we investigated the settlement pattern of immigrants in relation to their genetic relatedness to breeders. Then, we used data on social interactions among group members foraging at feeders to assess the occurrence and potential costs of different forms of aggression, and the factors that modulate aggression. Finally, we investigated the mechanism that breeders use to recognize their own offspring, by analysing the social interactions of breeders with own young and with cross-fostered young that were swapped as nestlings.

We used a model selection approach to investigate the relevance of different predictors that may influence aggressive interactions between individuals. On the basis of earlier studies, we predict that nepotism (i.e. the preferential treatment of relatives) and social dominance are the main factors that modulate aggression (Ekman & Sklepkovych 1994; Griesser 2003). If nepotism is a key driver of aggression and Siberian jays can assess fine-scale differences in relatedness, we expect breeders to increase their aggression towards less related immigrants, independent of their sex. However, if social dominance is a main driver of aggression, we expect that female nonbreeders receive more aggression than male nonbreeders, independent of differences in relatedness. Female nonbreeders have the lowest social

rank in groups because males are socially dominant over females.

Materials and methods

Data for this study were collected in a natural population of Siberian Jays, near Arvidsjaur in Northern Sweden (65°40 N, 19°0 E). Birds in this population have been studied intensely from 1989 onwards. We used behavioural observations collected during the nonbreeding season in 3 years (1999, 2008 and 2009) and complemented these observations with pairwise genetic relatedness analyses. In addition, we performed cross-fostering experiments in 2011 where one or two nestlings were exchanged between 24 nests (total 31 nestlings; mean \pm SE 1.29 \pm 0.09 nestlings cross-fostered per brood) when they were 6–12 days old (total nestling time: 24 days). In successful broods, we assessed the behaviour of breeders towards their own retained young (14 individuals in 11 groups) and retained cross-fostered young (six individuals in six groups) at feeders in July.

All individuals in the population were ringed with a uniquely numbered metal ring and 2–3 plastic colour rings for individual identification (for details, see Griesser *et al.* 2012). We took a small blood sample (\approx 50 μ L) for molecular sexing (Griffiths *et al.* 1998) and determination of genetic relatedness. The catching of birds, ringing, blood sampling, cross-fostering and behavioural experiments were performed under the licence of the Umeå ethics board (licence numbers A80-99, A45-04 and A50-11) and the licence of the Museum of Natural History, Stockholm.

To categorize the social relationship between group members (breeders, offspring, step offspring, immigrants), we used two different methods. Up to 2004, we followed reproduction during spring and marked all nestlings with a uniquely numbered metal ring in the nest, allowing us to recognize offspring after fledgling. Any unringed juvenile appearing in a group where we followed reproduction were then known to have immigrated from elsewhere. During 2005–2010, we did not follow the reproduction in the study population, and thus, we relied on molecular methods described below to determine relatedness among group members. All groups were visited twice per year: before reproduction in spring, and in autumn after dispersal and immigration. This allowed us to monitor changes in group composition and social rank of group members. In the Siberian jay, only the breeding pair reproduces and breeders are socially dominant over all other group members (Ekman *et al.* 1994), allowing the assessment of the social rank of individuals in the field.

Are breeders socially familiar with immigrants before their settlement?

We used data on between-group encounters with neighbours and dispersal distance of immigrants to assess whether breeders were socially familiar with immigrants before their settlement. We used data collected between June and July in 2000, 2003 and 2011 to assess the rate of between-group encounters before the dispersal of juveniles. Jays are year-round territorial and groups generally move as cohesive units through their territory (Griesser *et al.* 2006, 2008). To be able to follow groups, we caught fledglings in 36 groups 3–4 weeks after they left the nest and attached a radio-tag to at least one juvenile (see Griesser *et al.* 2008 for more details). Groups were followed during 30-min bouts, and we recorded all encounters with other groups. These data allowed us to assess the distance in which focal groups were socially familiar with individuals of other groups. We combined these data with earlier published data on juvenile dispersal distances for the same population (Griesser *et al.* 2014).

Behavioural assessment of aggression

We assessed the social interactions between group members on standardized feeders during 15-min or 30-min bouts between July and October, after the offspring dispersal phase (Griesser 2003). The feeders were placed at the edge of small forest openings close to a large tree, allowing group members to wait close to the feeder. Feeders were baited with two pieces of pig fat and had two horizontal branches allowing at least five individuals to forage simultaneously. Birds were attracted to the feeder by whistling. After a group arrived and started to forage, we assessed the aggressive interactions among group members using the following two categories (Ekman *et al.* 1994): displacements (an individual is approached and forced away from the feeder, or from the feeder surroundings, by another group member) or chasing events (an individual is chased by another group member in an aerial pursuit). The key difference between these two behaviours is that displacements only imply a small cost for the aggressor, and it is often associated with arriving at the feeder (an individual lands in the location of another individual, which in turn is forced away from the feeder). In contrast, chasing is more costly for the perpetrator because it pays the cost of actively chasing after the receptor and loses foraging time. We also recorded if individuals displayed submissive behaviour (i.e. gave begging calls and flapping wings as fledglings do when begging for food). This behaviour could either reduce the aggression displayed by other group members or could be given in

response to an aggressive action (Kutsukake & Clutton-Brock 2006). For all of these behaviours, we noted both the aggressor and the recipient.

We counted the total number of displacements and chasing incidents that a nonbreeder was subjected to. We used combined aggression scores of female and male breeders, because breeders cooperate when displaying aggression towards immigrants. Members of a breeding pair often take turns visiting the feeder, presumably to prevent immigrants from accessing the feeder, and the aggressive effort made by one breeder is dependent on the aggressive effort of its social partner (i.e. breeders never display aggression towards nonbreeders simultaneously; Ekman *et al.* 1994; Griesser 2003). In 1999, feeding bouts of 30 min were recorded with a video camera, and we recorded our verbal comments regarding the social interactions and individuals present on the feeder. From the videotapes, we extracted the social interactions among all group members, and measured the duration of 67 displacements and 20 chasing events. We could assess the duration of chasing events only when both the start and end of the interaction was recorded. In 2008, 2009 and 2011, we directly recorded all social interactions between foraging group members in the field using scoring sheets during 15-min feeding bouts. During the observations, we were positioned 10–15 m away from the feeder, allowing the birds to forage undisturbed while we were still able to see all behavioural details and identify all individuals.

Molecular methods and genetic relatedness analyses

DNA extraction, PCR amplification, sexing methods and the used microsatellites and their polymorphism are described in detail elsewhere (Griesser *et al.* 2014). We used three multiplexes with a total of 24 microsatellite markers that were tagged with fluorescent dyes. We assigned the social relationship between breeders and nonbreeders based on individual life histories (in 1999) or based on molecular relatedness estimates (in 2008, 2009), distinguishing between parent–offspring ($N = 30$) and breeder-immigrants ($N = 41$). In six groups, one of the breeders died after the young fledged. Offspring from these groups were categorized as retained offspring (in relation to the remaining parent) but as immigrant (in relation to the new breeder).

We determined the best performing genetic relatedness estimates (hereafter r) by comparing seven estimators: Dyad maximum likelihood (hereafter DyadML; Milligan 2003), Lynch and Li's estimator (hereafter LynchLi; Lynch 1988), Lynch and Ritland's estimator (hereafter LynchRd; Lynch & Ritland 1999), Queller and Goodnight's estimator (hereafter QuellerGt; Queller & Goodnight 1989), Trio maximum likelihood (hereafter

TrioML; Wang 2007), Ritland's estimator (hereafter Ritland; Ritland 1996) and Wang's estimator (hereafter Wang; Wang 2002), using the software COANCESTRY 1.0.1.2 (Wang 2011a). Analyses with the software GENEPOP (Rousset 2008) showed that the genetic structure (measured as F_{ST}) differed between 1999 and 2008–2009, while samples from 2008 and 2009 were not different from each other (Table S1, Supporting information). Thus, we calculated the r estimates separately for these two time periods. We used simulations in COANCESTRY to find the estimator that gave the most accurate r estimate compared to pedigree relatedness of parent–offspring pairs and showed the lowest variance for the sampled population (Csillery *et al.* 2006; Pemberton 2008; Santure *et al.* 2010; Wang 2011a; Taylor 2015). Estimators of r differ in a fundamental statistical property that might influence our analyses: they are either constrained (i.e. minimum relatedness is always 0; DyadML and TrioML) or unconstrained (all other r estimators). Thus, we choose both a constrained and an unconstrained r estimator. Simulations revealed that DyadML and Ritland were the most accurate r estimators (Table S2, Supporting information), while all assessed estimators had a high precision, reflect relative differences in relatedness among individuals (Table S3, Supporting information) and were highly correlated with each other (Pearson's $r > 0.83$) (Table S4, Supporting information). Thus, we used these two r estimators for our analyses. Using two estimators with different characteristics is conservative from the point of view of their statistical properties. Ritland is sensitive to rare alleles and consequently performs well for less related individuals (Wang 2011a). However, it is outcompeted by maximum-likelihood-based estimators, such as DyadML, in cases where large numbers of highly polymorphic makers are available (Wang 2011a). Data from 1999 showed that pairwise estimates DyadML's $r > 0.38$ reflected parent–offspring relationship for male breeders and $r > 0.32$ for female breeders. These thresholds were used to assign the kin relationship between breeders and nonbreeders in 2008 and 2009.

Statistical analyses

An important a priori assumption of our analyses is that relatedness between breeders and immigrants does not limit the settlement of immigrants. Behavioural observations showed that juvenile group members limit the settlement of immigrants while breeders do not actively prevent dispersers from settling on their territory (Griesser *et al.* 2008). We generated unique random pairs of male or female breeders and immigrants across the entire population to test this assumption. We analysed the distributions of random and observed

breeder-immigrant relatedness with a Kolmogorov–Smirnov two-sample test.

For the analysis looking into the factors affecting breeder aggression, we had data from 37 groups. The sample sizes in our data sets varied depending on the availability of relatedness data (female breeder/nonbreeder pairs: $N = 50$ immigrants and $N = 31$ retained offspring from 37 groups; male breeder/nonbreeder pairs: $N = 38$ immigrants and $N = 30$ retained offspring from 35 groups). We counted the number of displacements and chasing events during 30 min. In 1999, we compiled observations during 30 min, while in 2008 and 2009 during 15 min, and thus, we doubled the number of displacements and chasing events from 2008 and 2009 to have comparable data. We did not combine observations collected on different days (mean number of observations \pm SE with female breeder: 1.54 ± 0.08 ; with male breeder: 1.59 ± 0.08). Group composition often changed between observations as nonbreeders can move independently of the rest of the group (Griesser *et al.* 2006) or because individuals from other groups occasionally visited the feeder.

We used the *GLMMADMB* package (Fournier *et al.* 2012) in R version 2.15.0 (R Development Core Team 2013) to assess the effect of social relationship and genetic relatedness on the number of chasing events an immigrant experienced. Displacements occur opportunistically and only have a very low cost to the perpetrator (see below), and thus, we only analysed the number of chasing events. Furthermore, breeders almost never chase retained offspring, and therefore, we only included immigrants in the analyses. We used a model selection procedure to find the most suitable model to explain the observed responses. We report the parameter estimates obtained after averaging over the set of best fitting models ($\Delta AIC_c < 2$) using the package *MUMIN* (Bartoń 2012). Sets of analysed models (up to $\Delta AIC_c = 5$) are provided in the Supporting information.

Poisson distributed data often are overdispersed (i.e. the response variable exhibits a substantial number of zeros), but the *GLMMADMB* package cannot account for overdispersion. To confirm that our results were not biased by overdispersion, we fitted the models with the highest AIC_c using generalized linear mixed models with zero-inflated Poisson distributions in *MCMCGLMM* (Hadfield 2010). Using *MCMCGLMM* for a model selection approach is impractical as the running time for our data would take 3 months. All models were run for 6 500 000 iterations, with a 500 000 burn-in period and samples drawn every 500 iterations, with priors recommended in Hadfield (2014). The results from the *MCMCGLMM*-fitted models were qualitatively the same, confirming that the outputs from *GLMMADMB* are statistically solid.

We ran separate models for male and female breeders. All models included two random effects: individual identity and territory identity, to account for nonindependence of data points resulting from individuals sampled repeatedly and on the same territory. We included the following independent fixed terms in our statistical analyses: pairwise genetic relatedness between breeder and immigrant (separate models for Ritland and *DyadML*), number of submissive behaviours displayed by immigrants, group size, sex of the immigrant, age of the immigrant, age of the breeder, weighted breeding success of the territory (see below), habitat structure of the territory (see below) and year. Submissive behaviours can modulate aggression in social animals and were therefore included into the models. Group size could influence aggressive interactions because individuals in larger groups can be exposed to more aggression and experience more competitive conditions (Caraco 1979). Immigrant sex has been shown to influence within-group aggression in Siberian jays (Ekman & Sklepkovych 1994). Moreover, both the age of immigrants and breeders could modulate aggression given that in social species conflicts between nonbreeders and breeders increase with their age (Kutsukake & Clutton-Brock 2006). As all immigrants were assessed in the group where they initially immigrated as juveniles, the age of the nonbreeder corresponded to their tenure in the group, controlling for changes in aggression due to familiarity. Finally, we included two ecological key variables that relate to territory and habitat structure of the territory and influence the breeding success. Breeders on territories with a high breeding success could afford to invest more time into aggression. To quantify this effect, we used the weighted breeding success of a territory in a given year compared to the mean breeding success in the population (see Ekman *et al.* 2001 for detailed description of calculation). The habitat structure of a territory was characterized by the proportion of unmanaged forest on a territory. This measure has been shown to positively affect survival (see Griesser *et al.* 2006 for detailed description of assessment) and could influence social relationship among group members.

We compared the behaviour of breeders towards own young and cross-fostered young with Fisher's exact tests to assess whether Siberian jays use phenotypic cues to recognize own young independent of social cues. We assessed whether displacements (yes/no) or chasing events (yes/no) differed between own young ($N = 14$ in 11 groups; we only included one juvenile of each group in the analyses, randomly excluding one juvenile that did not receive aggression) and cross-fostered young ($N = 6$ in six groups). We used this analytical approach to ensure that we detected small differences in the behaviour towards

own young and cross-fostered young because parents only exceptionally display aggressive behaviours towards own young (Ekman *et al.* 1994).

Results

Social familiarity of immigrants

Between offspring fledgling and dispersal, Siberian jay groups encountered neighbour groups every 19.9 h (23 encounters during 457.6 h in the field) and a neighbour's neighbour group every 228.8 h (two encounters). Accordingly, groups meet a neighbour group about once a day and a neighbour's neighbour group about once every second week. (Siberian jays are active during 16 h per day in summer.) However, only seven of 734 ringed nestlings (including four individuals that were followed with the help of radio-tags) settled in a neighbour or neighbour's neighbour territory (Fig. 1). Thus, breeders were probably to be socially familiar only with a very small number of immigrants (<1%) before their settlement.

Settlement of immigrants in relation to breeder relatedness

Genetic relatedness between immigrants and breeders did not influence the settlement of immigrants. The distribution of observed pairwise genetic relatedness

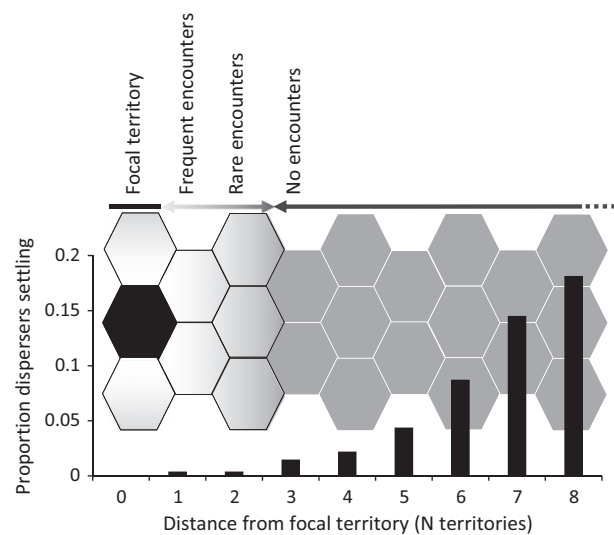


Fig. 1 Encounter rate of groups (focal territory in black; polygons represent territories) with direct neighbour (light grey polygons) and neighbour's neighbour groups (medium grey polygons) in relation to the distribution of dispersal distance of juvenile dispersers (black bars). Before the dispersal of juveniles in June and July, groups encounter their direct neighbours about once a day and their neighbour's neighbour about every second week. Within this range, <1% of dispersing juveniles settle.

between breeders and immigrants from the same group did not differ from the distribution of randomly selected breeders and immigrants (Fig. 2).

Aggression towards nonbreeders

On average, nonbreeders were displaced 4.2 times and chased 0.4 times per 30-min observation bout, and female nonbreeders were chased more often than male nonbreeders (Fig. 3). Breeders were more aggressive towards immigrants (6.5 displacements, 0.7 chasing events per 30 min) than towards retained offspring (1.3 displacements, 0.06 chasing events per 30 min) (Fig. 3), confirming earlier findings (Ekman *et al.* 1994). Immigrants fell into two distinct categories: they were aggressed either by breeders (i.e. they received $95 \pm 1.4\%$ (mean \pm SE) of displacements and $98 \pm 9.8\%$ of chasing events from breeders) or by other nonbreeders (i.e. they received $94 \pm 12.8\%$ of displacements and $100 \pm 0\%$ of chasing events from nonbreeders). Only one immigrant fell into this last category and was chased by another nonbreeder, and thus, we

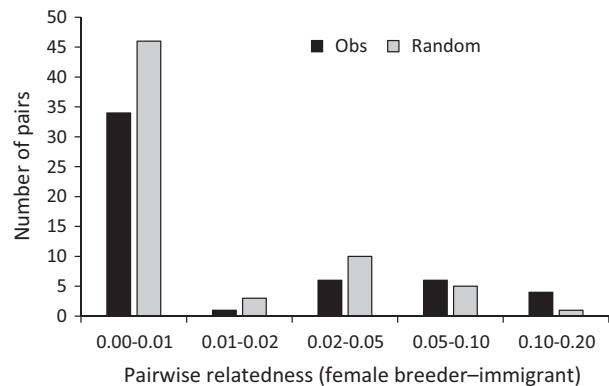
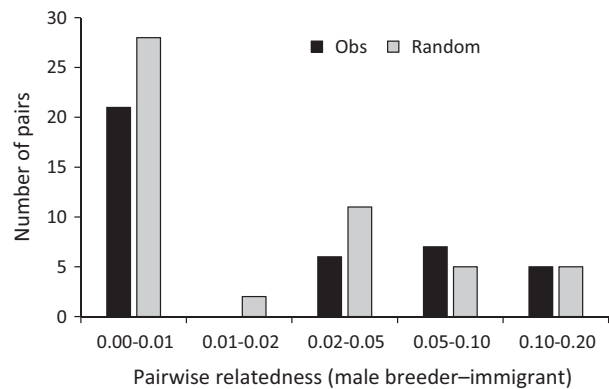


Fig. 2 Distribution of pairwise relatedness between observed pairs of breeders and immigrants (obs), and between randomly selected pairs of male breeder and immigrant (a) or female breeder and immigrant (b); Kolmogorov-Smirnov two-sample test: $D = 0.15$, $P = 0.64$ or Kolmogorov-Smirnov two-sample test: $D = 0.13$, $P = 0.71$).

excluded this individual from the analyses. Aggression exceptionally occurred between parents and offspring. In one group, the female breeder disappeared and was replaced by a new female 1–4 weeks before the behavioural sampling. The father chased his son 10 times during the 30-min observation, presumably to reduce the son's chances of pairing up with the new female.

Displacements and chasing events differed in their duration and the context in which they occurred. Most displacements took place immediately upon arrival of the perpetrator to the feeder (39 of 67 displacements; no additional time required for the perpetrator) or when the perpetrator changed its position on the feeder (22 of 67 displacements; mean duration of displacement \pm SE = 0.28 ± 0.15 s). Only in six occasions the perpetrator displaced a nonbreeder perched in the vicinity of the feeder (mean duration of displacement \pm SE = 0.55 ± 0.06 s). Thus, most displacements involved only a small cost for the perpetrator and did not interrupt its foraging. In contrast, chasing events were more costly for the perpetrator as they actively chased after the recipient ($N = 20$, mean duration \pm SE = 4.20 ± 3.66 s). Given the low cost and opportunistic nature of displacements and that breeders only exceptionally display aggression towards retained offspring, we focus in the subsequent analyses on chasing events involving breeders and immigrants.

Aggression towards immigrants was not uniform but modulated by genetic relatedness between breeders and immigrants. Breeders chased the least related immigrants most often in relation to male breeder relatedness (sum of Akaike weights = 1.0 both using DyadML and Ritland r estimators; Table 1, Fig. 4). Moreover, female immigrants received more aggression than male

immigrants (Table 1), and older male breeders displayed more aggression towards immigrants than younger male breeders (only Ritland r ; Table 1). However, relatedness between female breeder and immigrants did not modify aggression (Fig. 4), but these models confirmed that female immigrants received more aggression than male immigrants and that immigrants in groups living on more open territories receive more aggression (Table 1). The age of immigrants (corresponding to their tenure in the group) did not influence the aggression it received.

Kin discrimination of own and cross-fostered young

These results raise the question whether Siberian jays may use this ability to discriminate among own young and cross-fostered young. Thus, we compared the response of breeders when foraging together with own young and cross-fostered young. Parents did not behave differently towards their own young and cross-fostered young that had been swapped into the nest experimentally as nestlings. Only one male displaced an own young twice during 30 min but no other parents displaced or chased own or cross-fostered young (Fisher's exact tests comparing the presence/absence of breeder aggression towards their own and foster young; occurrence of displacements: $P = 1$; chasing events: $P = 1$).

Discussion

Our results suggest that Siberian jay breeders are able to recognize fine-scale differences in the genetic relatedness of nonbreeders of unfamiliar origin and modulate their aggression accordingly (Fig. 4). While a few species with high degrees of extra-pair paternity have evolved the recognition of first-order relatives (i.e. siblings) in the absence of social relatedness cues (Petrie *et al.* 1999; Mateo & Johnston 2000; Hain & Neff 2006), we show that kin recognition of socially unfamiliar individuals could be a more universal phenomenon than hitherto assumed, occurring in a species that is completely monogamous. More importantly, our results suggest that Siberian jay breeders show fine-scale relatedness discrimination in the absence of social relatedness cues, which to our knowledge has not been demonstrated in other vertebrates (Komdeur & Hatchwell 1999; Hatchwell 2010; Ihle & Forstmeier 2013).

Kin recognition in the absence of social familiarity may be more common than assumed because genetic relatedness has been suggested to affect extra-pair mate choice decisions (Arct *et al.* 2015). Many species live in kin groups (Drobniak *et al.* 2015) and interact with individuals of other groups. Thus, recognizing socially

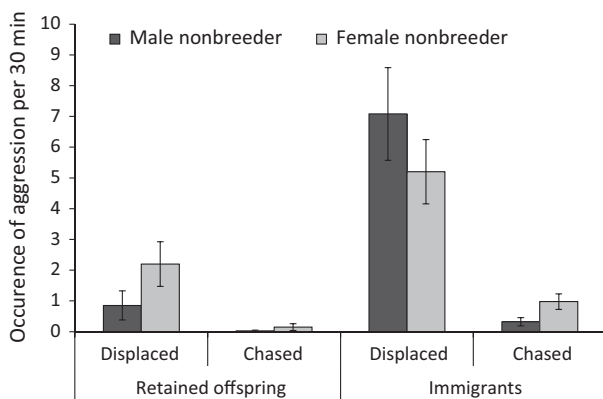


Fig. 3 Mean number of displacements and chasing events Siberian jay nonbreeders experienced during 30-min sampling observations (mean \pm SE) in relation to nonbreeder sex and social relationship (retained offspring, immigrants). Female nonbreeders experienced more aggression than male nonbreeders, and immigrants experienced more aggression than retained offspring.

Table 1 Factors affecting chasing events of immigrants displayed by breeders in Siberian jay groups using the two best genetic relatedness estimators r (DyadML, Ritland). Model selection and model averaging approach according to the AIC_C ($\Delta AIC_C < 2$). Factors with a sum of Akaike weights (ΣAIC_C weights) larger than 0.5 and standard error (SE) of estimates do not overlap 0 are highlighted in bold. Reference level of sex: female, year: 1999. Prop unmanaged forests = proportion unmanaged forests on a territory

	Estimate	SE	Adjusted SE	z-Value	P-value	ΣAIC_C	N models including variable
Male kinship – DyadML							
Intercept	1.19	0.23	0.24	5.00	0.0000		
DyadML	−9.26	3.69	3.77	2.46	0.01	1.00	3
Sex (m)	−1.23	0.51	0.52	2.36	0.02	1.00	3
Age nonbreeder	0.07	0.17	0.17	0.43	0.66	0.29	1
Age breeder	0.01	0.04	0.04	0.28	0.78	0.20	1
Male kinship - Ritland							
Intercept	0.56	0.37	0.37	1.50	0.13		
Ritland	−3.68	1.56	1.59	2.31	0.02	1.00	5
Sex (m)	−1.31	0.51	0.53	2.49	0.01	1.00	5
Age breeder	0.07	0.08	0.08	0.80	0.42	0.55	3
Age nonbreeder	0.06	0.17	0.17	0.38	0.71	0.27	2
Submissive behaviour	0.02	0.05	0.05	0.31	0.76	0.12	1
Age breeder × Submissive behaviour	−0.01	0.04	0.04	0.31	0.76	0.12	1
Female kinship – DyadML							
Intercept	0.61	0.65	0.65	0.94	0.34		
Sex (m)	−1.35	0.51	0.52	2.61	0.009	1.00	9
Prop unmanaged forests	−0.95	0.78	0.79	1.20	0.23	0.76	6
Age nonbreeder	0.17	0.32	0.32	0.51	0.60	0.32	3
Group size	0.04	0.10	0.10	0.36	0.72	0.18	2
Year (2008)	−0.06	0.28	0.28	0.23	0.81	0.17	2
Year (2009)	0.10	0.34	0.35	0.30	0.76		
Age breeder	−0.01	0.04	0.04	0.29	0.77	0.13	1
Submissive behaviour	0.00	0.02	0.02	0.18	0.85	0.07	1
Female kinship – Ritland							
Intercept	0.61	0.61	0.61	1.00	0.32		
Sex (m)	−1.35	0.51	0.52	2.59	0.009	1.00	12
Prop unmanaged forests	−0.98	0.81	0.82	1.20	0.23	0.74	8
Age nonbreeder	0.18	0.33	0.34	0.55	0.58	0.34	4
Ritland	0.33	2.54	2.55	0.13	0.90	0.22	3
Group size	0.03	0.09	0.09	0.31	0.76	0.14	2
Year (2008)	−0.05	0.25	0.25	0.20	0.84	0.13	2
Year (2009)	0.08	0.31	0.31	0.26	0.79		
Age breeder	−0.01	0.04	0.04	0.25	0.80	0.10	1
Submissive behaviour	0.00	0.01	0.01	0.16	0.87	0.06	1

unfamiliar kin can be an advantage when interacting with other groups (Griesser *et al.* 2009), or to avoid inbreeding (Komdeur & Hatchwell 1999). A study in long-tailed tits (*Aegithalos caudatus*) showed that decreasing genetic relatedness increases the willingness to invest in helping at the nest (Nam *et al.* 2010). However, long-tailed tits are socially familiar with potential helpers because neighbours forms large social groups outside the breeding season (McGowan *et al.* 2007). Similarly, in cooperatively breeding carrion crows (*Corvus corone*), nonbreeders that leave their natal territory join preferably groups with relatives, where cooperation results in indirect fitness benefits (Baglione *et al.* 2003).

While it was suggested that dispersing carrion crows recognize relatives based on social familiarity (Baglione *et al.* 2003), phenotypic kin recognition cues could be advantageous to discriminate relatives from nonrelatives in the absence of social familiarity.

Our results raise the question why Siberian jays have evolved fine-scale kin recognition for socially unfamiliar individuals. Siberian jays do not breed cooperatively (Ekman *et al.* 1994) but breeders display a high degree of nepotism during foraging and predator encounters (Griesser 2003, 2008, 2009; Griesser & Ekman 2004, 2005). Thus, inclusive fitness benefits could play a role for the evolution of fine-scale kin recognition in this

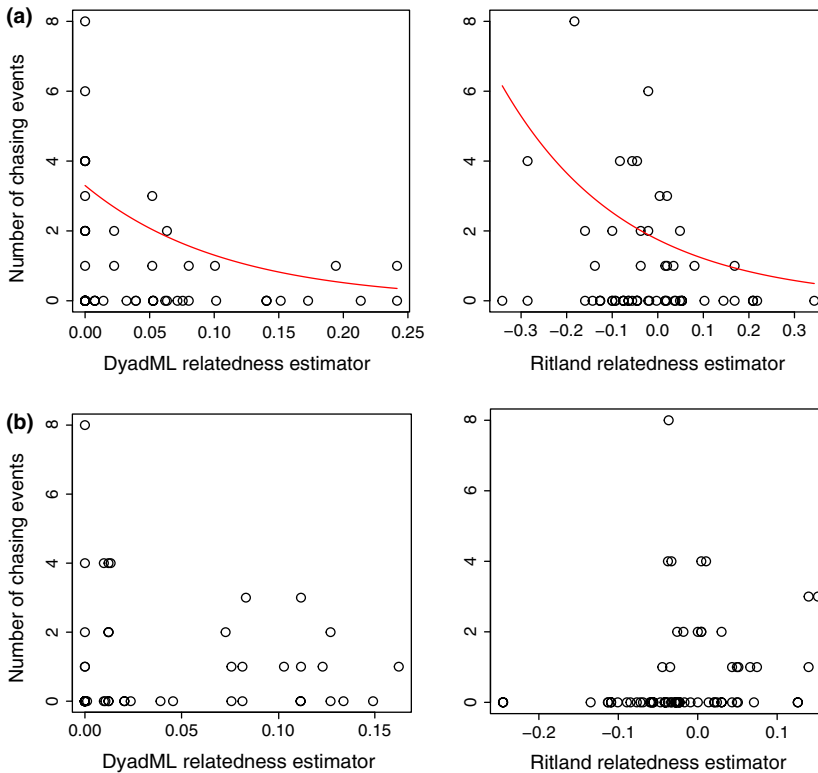


Fig. 4 Number of chasing events experienced by immigrants during 30-min sampling bouts in relation to (a) male breeder and (b) female breeder relatedness (DyadML, Ritland) between breeders and immigrants in the Siberian jay. More unrelated immigrants are exposed to significantly more chasing events.

species. Jays can encounter socially unfamiliar, more distant relatives at carcasses of herbivores killed by large predators (brown bear *Ursus arcticus*, wolf *Canis lupus*, wolverine *Gulo gulo*), hunters or cars, allowing to modulate the level of between-group aggression depending on their relatedness.

Kin recognition in the absence of social cues can provide an advantage when extra-pair paternity obscures relatedness among close relatives. This factor is not of importance in Siberian jays, since they are socially and genetically monogamous. So, why do breeders expose more unrelated immigrants to higher levels of aggression? While immigrants are potential future mates (Ekman *et al.* 2001), their presence can be costly and increase the rate of conflicts during the breeding season, reducing nestling condition (Griesser *et al.* 2008). High levels of aggression limits the access to resources of immigrants (Ekman *et al.* 1994; Griesser 2003), lowering their feather quality compared to immigrants that experience low levels of aggression (Panagakos 2009). Low feather quality is associated with an increased risk of being killed by a predator (Griesser *et al.* 2006). Besides, high levels of aggression cause immigrants to spend more time on their own, which also can contribute to a higher risk of predation (Griesser *et al.* 2006; Griesser 2013). Thus, high levels of aggression might indirectly increase the mortality of more unrelated immigrants.

Breeders often tolerate opposite-sex immigrants when foraging together (Ekman & Sklepkovych 1994) because they are potential future mates. Interestingly, only male but not female relatedness modulated aggression. This pattern most likely reflects dominance hierarchies in Siberian jay groups (Ekman & Sklepkovych 1994). Males are dominant over females and breeders are dominant over nonbreeders, while sometimes male nonbreeders can be dominant over female breeders (Ekman & Sklepkovych 1994). Thus, it is more costly to display aggression towards male than female immigrants and accordingly, female immigrants receive more aggression than male immigrants. A number of breeders did not show aggression towards highly unrelated immigrants. While this could be interpreted as kin recognition errors, it may be linked to the behaviour of the immigrants. Immigrants are not usually tolerated feeding simultaneously with breeders (Griesser 2003), and breeders might be particularly aggressive towards immigrants that try to access the feeder in their presence (Ekman & Sklepkovych 1994). Thus, immigrants that do not access a feeder in the presence of breeders are much less likely to be displaced or chased.

Our analyses depend on the accuracy of the r estimates, which is confirmed by simulations (simulated r estimates for parents–offspring = 0.451 (year 1999) and 0.471 (years 2008/2009) for DyadML; 0.451 (year 1999)

and 0.460 (years 2008/2009) for Ritland; Table S2, Supporting information). These two r estimators have a variance for immigrants of 0.003–0.015 (Table S2, Supporting information), and thus, the uncertainty in the r estimates is of smaller magnitude than the relatedness range between breeders and nonbreeders. The variability in r estimates of retained offspring ($r = 0.32$ – 0.6 for DyadML) reflects the fact that we assessed relatedness based on allele frequencies estimated from a nonrandom sample of the population (including family groups) and not population-wide allele frequencies. Generally, r estimates of true offspring based on identical-in-state alleles often deviate from 0.5 (Wang 2011b) because individuals can share the same allele without having a common pedigree (i.e. alleles are identical-in-state but not identical-by-descent), or when reference allele frequencies are biased as is the case in structured populations with nonrandom mating (Wang 2011b).

A central assumption of our study is that breeders are not socially familiar with the immigrants before their settlement. All immigrants used in our analyses immigrated into the study population as juveniles and dispersed within 6–8 weeks after fledgling from their natal group. Given that the dispersal distance of almost all juveniles is much larger than the distance over which groups are socially familiar with other groups, only a very small proportion of immigrants are expected to be socially known by group members before they settled (see above, Fig. 1). Also, it seems unlikely that behavioural traits linked to dispersal and settlement, such as the boldness of the disperser, could create a link between dispersal distance and aggression received from the breeders. Dispersal and settlement decisions are primarily driven by retained juveniles or immigrants juveniles that have settled already. They chase away dispersing juveniles, thereby preventing them from settling, while breeders do not chase dispersers off their territory (Griesser *et al.* 2008). As dispersal in Siberian jays resembles a random walk (Griesser *et al.* 2008), the travelled distance and the direct distance between the natal territory and the territory of settlement are poorly correlated. Thus, any trait linked to dispersal distance would be associated with huge uncertainty. Rather, breeders are probably to use a phenotypic cue or self-referent phenotype matching to judge the level of relatedness of socially unfamiliar individuals.

Siberian jays have evolved different mechanisms to differentiate between their own offspring and socially unfamiliar individuals. Breeders do not discriminate between cross-fostered young and their own young, but gradually increase their aggression towards immigrants with decreasing levels of genetic relatedness. Many bird

species, and most likely also Siberian jays, use contextual cues to recognize their own offspring (i.e. associative learning based on familiarity; Penn & Frommen 2010), a mechanism that is exploited by brood parasites such as cuckoos. Cuckoo nestlings are treated as own young despite that they look very different than own young, and only exceptionally give a fitness advantage to the parasitized brood (Canestrari *et al.* 2014). However, to our knowledge no study has investigated kin recognition mechanisms across different contexts, but this could provide a valuable tool to understand the costs and benefits of different kin recognition mechanisms. Given the high fitness costs of erroneously rejecting an own offspring, even species with extra-pair paternity have only rarely evolved familiarity-independent kin recognition rules for their own offspring (Kempenaers & Sheldon 1996; Shizuka & Lyon 2010). Recognition of socially unfamiliar first-order relatives can be based on olfactory cues (fish, mammals, birds; Mateo & Johnston 2000; Hain & Neff 2006; Krause *et al.* 2012), acoustic cues (birds; Sharp *et al.* 2005) or possibly visual cues (birds; Petrie *et al.* 1999). As we did not address the proximate kin recognition mechanism in our study, the cross-fostering experiments only exclude that Siberian jay parents rely on genetic cues to recognize their offspring.

To conclude, our results show that a social, non-promiscuous bird species can recognize fine-scale differences in genetic relatedness of socially unfamiliar individuals. Kin recognition is a critical element for kin cooperation, and in species where kin cooperate but the degree of relatedness among group member varies (Griesser *et al.* 2009; Drobniak *et al.* 2015), individuals benefit from discriminating related individuals from unrelated ones. Previous studies have shown that promiscuity can facilitate the evolution of first-order kin recognition in the absence of associative learning (Hain & Neff 2006). However, social animals do not only cooperate during reproduction. Kin cooperation may occur during foraging, when facing predators, or in territory acquisition (Covas & Griesser 2007; Hatchwell 2010). Thus, it may be advantageous to recognize related (or unrelated) individuals in general, and as our data suggest, animals may be capable of fine-scale kin recognition in the absence of social cues.

Acknowledgements

We thank Folke and Maj Lindgren for sharing their knowledge about the jays, and Gunnar and Ingrid Pavval for their hospitality at Lappugglan. The journal club of the Anthropological Institute, Jan Ekman, Livia Gerber, Simone Webber, Michael Krützen, Staffan Bensch and five anonymous reviewers provided helpful comments on the analyses and the manuscript. Our research was supported by the Swedish Natural Research

Council (to Jan Ekman), the Stiftelsen för Zoologisk Forskning (to MG and PH) and the Swiss National Science Foundation grant number PPOOP3_123520 and PP003_150752 (to MG).

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M.G. conceived the study; M.G. and P.H. collected the field data; P.H. and M.G. analysed the molecular data; S.D. and M.G. performed the statistical analyses; M.G., C.V., S.D. and P.H. wrote the manuscript.

Data accessibility

The following data item are deposited in Dryad (doi:10.5061/dryad.7j908): used microsatellites, microsatellite data, social interactions with own and cross-fostered young, duration of aggression, between-group encounters, dispersal data, main data set assessing the link between genetic relatedness and aggression and used r code. We adhere to the data sharing policies outlined in Mills *et al.* (2015).

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 F_{ST} estimates for all used loci and years (upper right half, in bold), and pairwise P -values based on 3000 permutations (bottom left half, in italics). Indicative adjusted nominal level (5%) for multiple comparisons is $P = 0.0167$, calculated in FSTAT 2.93 (Goudet *et al.* 1996).

Table S2 Performance of different relatedness estimators (r) based on Siberian jays included in our analyses.

Table S3 Observed mean values and variance of the different estimators for parent-retained offspring and breeder-immigrants dyads (values for both male breeder vs nonbreeder and female breeder vs nonbreeder and thus the sample size is larger than the number of retained offspring respectively immigrants).

Table S4 Person's product-moment correlation coefficients (Pearson's R) between the different relatedness estimates for female breeder – nonbreeder dyads (upper right half) and male breeder – nonbreeder dyads included in our analyses (bottom left half).