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Original Article

Direct fitness benefits and kinship of social foraging groups in an Old World tropical babbler

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Molecular studies have revealed that social groups composed mainly of nonrelatives may be widespread in group-living vertebrates, but the benefits favoring such sociality are not well understood. In the Old World, birds often form conspecific foraging groups that are maintained year-round and offspring usually disperse to other social groups. We tested the hypothesis that nonbreeding group members are largely unrelated and gain direct fitness benefits through breeding opportunities (males) and brood parasitism (females) in the tropical gray-throated babbler, *Stachyris nigriceps*, in Malaysian Borneo. Babblers foraged in social groups containing one or more breeding pairs (median = 8 group members of equal sex ratio), but group members rarely assisted with breeding (9% of 67 breeding pairs had a third helper; exhibiting facultative cooperative breeding). Although 20% of 266 group member dyads were first-order relatives of one or both members of the breeding pairs, 80% were unrelated. Male group members gained direct fitness benefits through extrapair and extra-group paternity (25% of 73 offspring), which was independent of their relatedness to the breeding pair and increased with decreasing group size. In contrast, females did not gain direct fitness benefits through brood parasitism. The low levels of relatedness and helping in social groups suggest that most group members do not gain indirect fitness benefits by helping to raise unrelated offspring. These findings highlight the importance of examining benefits of sociality for unrelated individuals that largely do not help and broaden the direct fitness benefits of group foraging beyond assumed survival benefits.

Key words: **facultative cooperative breeding, genetic mating system, Old World tropics, parentage, relatedness.**

INTRODUCTION

The evolution of group living, in which individuals of the same species live together in stable associations, has been of long-standing interest to behavioral ecologists studying a wide range of vertebrate taxa (Krause and Ruxton 2002; Ward and Webster 2016). This body of work—largely focused on cooperative breeders—has enhanced our understanding of the fitness benefits of sociality (Solomon and French 1997; Cockburn 2004; Russell 2004; Koenig and Dickinson 2016). Cooperative breeding groups often form when offspring delay dispersal and remain on their natal territory (Brown 1987; Koenig et al. 1992; Hatchwell 2009), resulting in groups mainly composed of a breeding pair and nonbreeding relatives that assist their parents in raising siblings (e.g., Florida scrub-jay, *Aphelocoma coerulescens*, Woolfenden and Fitzpatrick 1984; dwarf-banded shellie, *Neolamprologus multifasciatus*, Taborsky 2009; wolf, *Canis lupis*, Stenglein et al. 2011). Thus, cooperative breeding in kin groups is primarily explained by kin selection and indirect fitness (Green et al. 2016). However, recent molecular studies have revealed that cooperative breeding groups commonly contain nonrelatives (e.g., 44% of cooperatively breeding birds, Riehl 2013). For example, group members could help in raising unrelated offspring when the dominant breeders change and helpers continue to raise the offspring of replacement dominants (e.g., Lake Tanganyika cichlids, Dierkes et al. 2005). Moreover, stable associations among a mix of relatives and nonrelatives in contexts other than breeding may be extensive (Taborsky et al. 2016). In such systems with complex social structures, studies have increasingly emphasized the importance of direct fitness benefits for maintaining associations between nonrelatives (Riehl 2013; Taborsky et al. 2016b).

Group membership could confer direct fitness benefits of both increased survival and reproduction for unrelated individuals.

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Members that associate during the nonbreeding season to forage in groups can increase their survival through improved foraging success and shared vigilance for predators such as winter grouping of the long-tailed tit, *Aegithalos caudatus* (Napper and Hatchwell 2016) and Siberian Jay, *Perisoreus infaustus* (Griesser et al. 2006; Griesser 2013), and mixed-species winter foraging flocks in the New World tropics and temperate zone (Jullien and Clobert 2000; Sridhar et al. 2009; Sridhar and Shanker 2013). Members of cooperative breeding groups that associate during the breeding season can acquire skills relevant to parenting, inherit mates or breeding territories, and gain access to current or future breeding opportunities (Cockburn 1998; Cockburn 2004; Taborsky et al. 2016a). However, the fitness benefits of group membership are less clear for conspecific foraging groups that remain together year-round, during both the nonbreeding and breeding seasons, which is an unusual characteristic of group-living species in the Old World tropics. For example, when unrelated individuals remain in the foraging group during the breeding season but provide little to no help in breeding, how is this structure maintained? Although year-round foraging groups are prevalent in the Old World tropics, little is known about the composition of these social groups, the relatedness of group members, or the fitness benefits gained by group members. Thus, studying such populations could reveal fitness advantages that have otherwise been overlooked. In particular, group members might gain access to breeding opportunities within or even among social foraging groups through extrapair paternity, when individuals mate outside of their social pair bonds.

Male group members may have few opportunities for extrapair paternity because of reproductive competition within groups or incest avoidance. Generally, competition increases with decreasing genetic relatedness between same-sex group members (Whittingham and Magrath 1997; Magrath et al. 2004; Raihani and Clutton-Brock 2010; Nonacs and Hager 2011; Nelson-Flower and Ridley 2016). Reproductive sharing is expected to also decrease with the relatedness of potential breeders to avoid deleterious inbreeding (Magrath and Heinsohn 2000; Magrath et al. 2004). Alternatively, group augmentation theory suggests that male breeders should share reproduction to encourage unrelated group members to join when the benefits of increased group size or cooperative parental care outweigh the costs of losing some paternity (Kokko et al. 2001; Riehl 2013; Kingma et al. 2014).

Female group members could gain direct fitness benefits through both increased survival and more opportunities to reproduce. In social systems with joint-female nesting, more than one pair defends a group territory and females lay eggs in a shared nest (e.g., Taiwan yuhina, *Yuhina brunneiceps*, Yuan et al. 2004). In social systems with plural breeding, multiple females belonging to a group that share a territory build a nest to lay their own eggs (e.g., Mexican jay, *Aphelocoma ultramarine*, Brown and Brown 1990). Joint-female nesting primarily occurs in social groups composed of unrelated females (Vehrencamp 2000), whereas plural breeding is more common when female group members are highly related (Keller and Reeve 1994). Another route for females to gain direct fitness is by surreptitiously laying their own egg in the female breeder's nest or extragroup female's nest (conspecific brood parasitism; Andersson 2001).

In this study, we combined behavioral and molecular data to provide a first description of the social and genetic mating system of the gray-throated babbler *(Stachyris nigriceps)*—a resident of tropical submontane forests across Southeast Asia. The gray-throated babbler is an Old World species that forages in social groups year-round with conspecifics that likely are not close kin and appeared to rarely breed cooperatively. We suspected that their social groups contained nonrelatives because detection rates of birds of this species were quite high (Martin et al. 2017) and, yet, adults banded as nestlings were rarely observed with their natal groups and instead resighted with other groups (T.E.M., unpublished data). Therefore, traditional explanations for sociality might not fit this species' unusual lifestyle. We test the hypothesis that nonbreeding group members gain direct fitness benefits through extrapair and extragroup paternity (males) and conspecific brood parasitism (females), and then examine associations between paternity, genetic relatedness, and group size.

MATERIALS AND METHODS

Study species

The monomorphic, gray-throated babbler is a common resident of the tropical submontane forests of Northeast Indian subcontinent and southern China, Southeast Asia, Sumatra and Borneo (Collar and Robson 2007a; Myers 2009). The few babblers (Family Timaliidae) that have been studied exhibit striking diversity in their social behaviors and mating systems (Collar and Robson 2007b; Moyle et al. 2012). The gray-throated babbler is highly social and lives in social groups year-round. During the breeding months (December–August), smaller social groups of 5–8 individuals forage together in the understory. When social groups encounter each other, they will join together without conflict and form much larger, temporary groups of up to 25 individuals, even during the breeding season, but remain as separate and distinct groups (T.E.M., personal communication). These larger groups are more commonly observed during the nonbreeding months (Collar and Robson 2007a; Myers 2009).

Gray-throated babblers have been described as facultative cooperative breeders based on observations of up to 3 individuals attending some nests (Collar and Robson 2007a; Myers 2009). Females build dome nests, with assistance from males and occasionally from a third group member (T.E.M., personal observation). Nests are typically placed on the ground along banks and steep slopes and 1–3 m above ground frequently in spiny palms (genera *Calamus* and *Daemonorops*), and occasionally >4 m (T.E.M., unpublished data; Borneo). Females lay eggs on consecutive days (mean ± 1 SD; clutch size = 2.93 ± 0.29 eggs, range = 2–3 eggs, n = 217 clutches). Both males and females participate in incubation for approximately 16 days (Martin, Oteyza, Boyce, et al. 2015) and provision their nestlings at the nest for approximately 10 days (Martin, Oteyza, Mitchell, et al. 2015). Typically, a dominant breeding pair separates from their social group once they initiate breeding and remain largely on their own while nesting (T.E.M., personal observation). However, the breeding pair regularly joins their social group when group members forage near the nest, but only move with the group for short distances. The social group will often remain near the nest during nest building and egg laying, enabling the breeding pair to forage with their social group. Such behaviors around the female breeder's fertile stage may provide opportunities for group members to gain extrapair paternity within the group.

Field methods

We conducted a 6-year parentage study of a banded population of gray-throated babblers as part of a larger study of life histories of the bird community in Kinabalu Park, Sabah, Malaysian Borneo (6° N, 116° E); 2010–2015 (Martin, Oteyza, Boyce, et al.

2015; Martin, Oteyza, Mitchell, et al. 2015). Kinabalu Park consists of intact tropical forest from 400–4100 m and is one of the world's biodiversity hotspots designated as a World Heritage Site. The study area encompassed 7 study plots in lower montane forest from 1450–1950 m. The forest within this elevation zone is dense and contains a rich assemblage of plant taxa in the understory with a canopy reaching 25 m (Kitayama 1992; Nor 2001).

During the primary breeding season (February–June), we captured, color-banded, and collected blood samples from adults and nestlings, and monitored nesting attempts. We captured adults in mist-nets and marked each adult with a unique combination of colored leg bands and a numbered metal band to facilitate identification of social group members. Nestlings were handled at the nest and marked with a metal band (Gey Band and Tag Company; Norristown, PA), typically 6–7 days posthatching. Small blood samples (20–70 µL) were collected from the brachial vein and stored in lysis buffer (White and Densmore 1992) for sexing and parentage analyses. We found nests from parental behavior and systematic searching. The breeding pair and potential helpers were determined through repeated observations of banded individuals building and attending nests during the incubation and nestling stages during nest monitoring (every 1–3 days throughout all nest stages; once a day during egg laying to document potential conspecific brood parasitism and twice daily near hatch and fledge dates) and from video recordings (see "Parental activity" for details).

Group size and composition

Social foraging groups were defined as stable groups of individuals that foraged together in the same area during the breeding months (hereafter, social groups) (Cockburn 2004). We determined group size and composition by observing social groups repeatedly over the breeding season during daily nest searching and monitoring activities on each study plot (social groups were not monitored during the nonbreeding season). Resighting and detection rates of this species were quite high (Martin et al. 2017). We resighted color-banded individuals and recorded associated group members regularly, such that group membership was clear. Although small social groups do occasionally combine while foraging during the breeding season, these larger groups are transitory and quickly separate to spatially distinct areas. We report the size and composition of 30 social groups, in which all group members were color-banded. Sample sizes varied slightly among analyses because of missing genetic data for female breeders, male breeders, group members, and/or offspring (full details are given in Supplementary Table S1).

Parental activity

We recorded parental activity of the breeding pair and identified potential helpers at nests using video recordings taken during both the incubation and nestling stages for the first 6–8 h of daylight, starting within 30 min of sunrise: 2010–2014. Video cameras (Hi8 handycam camcorder, Sony Corporation; New York, NY) were mounted on tripods and camouflaged, set to view the nest entrance (optical zoom of 30×), and placed approximately 2–10 m from nests. To avoid behavioral disturbance, video cameras were left unattended. Parents resumed activities at the nest soon after camera placement. For each nest visit during the 6–8 h recordings, we confirmed the identity of the individual attending the nest based on its color band combination, and recorded its arrival and departure times during incubation, brooding, and parental provisioning (Martin et al. 2007; Martin et al. 2011). Parental provisioning rates were quantified as the total number of feeding trips per hour for each individual observed at the nest. As a basis for our knowledge of helping at the nest, we transcribed 112 recordings of 72 nests during the incubation stage for a total of 662 total incubation hours, and 210 recordings of 85 nests during the nestling stage for a total of 1231 total nestling hours.

Group and offspring sex ratio

We used molecular methods to determine the sex of group members and offspring. Molecular sexing was based on constant size differences between introns of the CHD-*W* and CHD-*Z* genes and the presence of female-specific fragments. Genomic DNA was extracted from whole blood with the BioSprint 96 Tissue DNA Kit (Qiagen, Valencia, CA). Sex was determined by amplifying 1 µL of genomic DNA from each individual with highly conserved primers, P2 and P8, that anneal to exonic regions flanking the introns in a 10 µL polymerase chain reaction (PCR) (Griffiths et al. 1998). The PCR products were size-sorted on an Applied Biosystems (ABI) 3130 Genetic Analyzer run with the GeneScan 500 base pair ROX internal size standard (ABI) and scored using Genemapper v.4.1 (ABI). Both sexes carry the CHD-*Z* gene (338 base pairs), but only females, the heterogametic sex, carries the CHD-*W* gene (386 base pairs). To verify the accuracy of our methods, we assayed equal numbers of adults of known sex based on the development of the cloaca or vascularization of the brood patch (n = 12 of each sex).

We followed the methods described in Neuhauser (2004) to test whether sex ratios of social groups (excluding the breeding pair) and offspring sex ratios differed from parity. Neuhauser's method is more robust than a Wilcoxon Rank Sum test for quantifying bias in sex ratios because it accounts for lack of independence among group members and among nestlings in a brood. We excluded 2 social groups with unbanded adults of unknown sex from analyses of the sex ratios of group members. We excluded 4 broods from analyses of offspring sex ratio because at least one offspring in the brood was not sampled (i.e., not bled). Analyses were conducted in R v.3.2.1 (R Development Core Team 2017).

Group relatedness

We genotyped 138 offspring from 56 broods and 112 sampled candidate parents (53 adult females and 59 adult males, including putative breeders and group members) associated with 37 monitored social groups at 8 polymorphic microsatellite loci isolated from the gray-throated babbler (Kaiser et al. 2015). We amplified from 1 µL of genomic DNA from each individual for each locus in a 10 µL PCR following previously described methods (Kaiser et al. 2015). The PCR products were size-sorted on an ABI 3130 Genetic Analyzer and run with the GeneScan 500 base pair ROX internal size standard. We scored alleles at each locus by visually confirming automated scores generated by Genemapper v.4.1 and repeated PCRs at homozygous loci to verify genotypes and to assess genotyping error.

We estimated average pairwise genetic relatedness for 4 types of relationships among breeding pairs, group members, and offspring by calculating Queller and Goodnight's r (Goodnight and Queller 1999) using KINGROUP v.2.0 (Konovalov et al. 2004). We tested whether 1) breeding pairs of each social group were nonrelatives, 2) group members were first-order relatives (parent/offspring or full siblings) of the female or male of the breeding pair, and 3) group members were first-order relatives (full siblings) with other group members or offspring (parent/offspring or full siblings). For these analyses, we tested the primary hypothesis that dyads (female and male breeders, breeders and group members, group members, and group members and offspring) were nonrelatives (relatedness of the mother [r_m] = 0, relatedness of the father [r_p] = 0) against a null hypothesis of first-order relatives (mother/offspring: $r_m = 1$, $r_p = 0$; father/offspring: $r_m = 0$, $r_p = 1$; full siblings: $r_m = 0.5$, $r_p = 0.5$). We ran 10,000 simulations to calculate the significance of log likelihood ratios ($P < 0.05$). When pairwise log ratios were greater than the 95% critical log likelihood ratio, we rejected the null hypothesis. If we failed to reject the null hypothesis, indicating that the dyads were related, we tested the primary hypothesis that dyads were first-order relatives against a null hypothesis of second-order relatives (maternal half siblings: $r_m = 0.5$, $r_p = 0$; paternal half siblings: $r_m = 0$, $r_p = 0.5$). The critical log likelihood ratios for each set of hypotheses and their associated Type II error rates at $P < 0.05$ are given in Supplementary Table S2. We calculated average pairwise genetic relatedness estimates for each type of relationship dyad. Sample sizes of female breeder/group member dyads and male breeder/group member dyads differed because not all female and male breeders in social groups were banded and/or sampled. For group members that were related to one of the breeders, we conducted chi-square tests for female and male group members separately to examine whether group members were more likely to be relatives of the same-sex breeder.

Parentage and kinship assignment

We conducted maternity (77 offspring from 31 broods) and paternity (73 offspring from 29 broods) analyses for each breeding season separately for offspring from social groups in which we banded and sampled both social parents (61 offspring), only the social mother (16 offspring), or only the social father (12 offspring) using CERVUS v.3.0, which uses a maximum likelihood-based approach to infer parentage (Marshall et al. 1998; Kalinowski et al. 2007). CERVUS calculates the natural logarithm of the likelihood ratio (LOD score), which provides the likelihood of parentage of each candidate parent relative to a random female or male in the population for each offspring. CERVUS uses simulations of the allele frequencies of adults in the population to calculate critical differences in LOD scores between the most likely mother and father and all other candidate parents to assign parentage at 95% confidence. We used simulations to calculate critical LOD scores for maternity and paternity considering 1) all candidate parents sampled in the population and 2) only candidate parents from within the group. Simulations take into account the average number of candidate parents per offspring and the proportion of candidate parents sampled. Therefore, the number of candidate parents in simulations of parentage using all candidate parents sampled in the population included 20% more than the total number of females or males associated with sampled social groups to account for unsampled individuals in the population from unmonitored social groups (Berg 2005; Riehl 2012). The number of candidate parents in simulations of parentage using only candidate parents from within a group included one more individual than the maximum number of female or male group members to account for parentage by unsampled individuals (2 groups contained one unsampled group member) (Richardson et al. 2001). We simulated maternity and paternity for 10,000 offspring (simulation parameters given in Supplementary Table S3).

We determined maternity and paternity of offspring using a 2-step approach. We first ran the maternity analysis including all candidate mothers sampled in the population. If allelic diversity was inadequate to assign offspring because of high relatedness between candidate females with zero mother–offspring mismatches, we assessed maternity considering only females from within the group (Blackmore and Heinsohn 2008; Riehl 2012). We assigned paternity following this same approach. Paternity analyses included known mothers for offspring based on maternity results, when possible.

We assessed CERVUS assignments using likelihood scores and developed decision rules for assigning parentage in this species. For parentage analyses we evaluated CERVUS assignments using pair LOD scores, which statistically distinguishes among nonexcluded candidate parents. For paternity analyses with known mothers, we evaluated CERVUS assignments of fathers using trio LOD scores, which statistically distinguishes among nonexcluded candidate males while considering the genotypes of the known mother. Briefly, if the social parents had a high likelihood score but mismatched the nestling at one or 2 loci, we investigated the possibility of null alleles or mistyping by repeating PCRs at mismatched loci and rescoring the alleles. We found no evidence of null alleles in a subsample of adult females using Micro-Checker v.2.2.3 (Van Oosterhout et al. 2004). We accepted the CERVUS assignment of the social parents if they mismatched at ≤1 locus. A nestling was considered to result from an extrapair parent if a social parent was not listed as a candidate parent by CERVUS (because of a negative pair or trio LOD score) or mismatched the nestling at ≥2 loci. In these cases, we identified the extrapair parent as the female or male that mismatched at ≤1 locus and that had the highest pair or trio LOD score. In some cases, no candidate parent matched the nestling's genotype (all had ≥2 mismatches with the nestling). We considered these nestlings to have been the result of an unsampled mother or father outside of the social group (i.e., extra-group parent). The combined nonexclusion probability for the set of 8 microsatellite loci was 0.008 for the mother and 0.064 for the father.

We used 2 methods of sibship reconstruction (65 offspring from 28 broods) to identify extrapair or extra-group offspring from nests in which we did not have genotypes for the social parents (49 of 138 offspring) or the social father (16 of 138 offspring). The presence of half siblings in a brood indicates multiple mating. First, we conducted maximum likelihood partitioning of nestlings into full sibling, half sibling, and unrelated clusters using COLONY 2.0 (Wang 2004). We allowed for a mating system with multiple maternity and paternity within broods with the possibility for inbreeding and used a genotyping error rate of 0.025% (Wang 2004). We used allele frequencies obtained from CERVUS. In the analyses, we included females and males as candidate parents for each offspring if they were adults when the young were hatched. To determine the confidence levels for assignments of the 49 siblings with no parental genotypes, we analyzed offspring from nests for which we had genotypes for both social parents and for which the sibling relationships (full siblings and half siblings) were known (unambiguous CERVUS assignments). Known sibling relationships were supported by probabilities of at least 0.9 in COLONY, which was the probability used to assume sibling relationships were correct. Second, we tested the primary hypothesis that offspring were full siblings ($r_m = 0.5$, $r_p = 0.5$) against a null hypothesis of maternal half siblings ($r_m = 0.5$, $r_p = 0$) or paternal half siblings ($r_m = 0$, $r_p = 0.5$) using likelihood ratio tests implemented in KINGROUP. We ran 10,000 simulations to calculate the significance of likelihood ratios ($P < 0.05$) (Supplementary Table S2). We calculated average pairwise genetic relatedness estimates for assignments of mother/offspring dyads and father/offspring dyads that were in agreement from parentage analyses using both CERVUS and COLONY. We calculated average pairwise genetic relatedness estimates for full sibling dyads and half sibling dyads that were supported by probabilities ≥0.9 from sibling reconstruction in COLONY.

Ethical note

This study was conducted under the auspices of the University of Montana IACUC protocol #059-10TMMCWRU and Smithsonian National Zoological Park Approval letter #12–30. We followed approved protocols to capture, handle, band, and sample gray-throated babblers. All work was performed under scientific permits from the Sabah Biodiversity Council. All procedures performed in this study were in accordance with the ABS/ASAB guidelines for the ethical treatment of animals in behavioral research. Sampling and processing had no discernable negative impacts on individuals. Behavioral observations did not disrupt the normal activities of individuals.

Statistical analyses

We examined the associations between extrapair paternity, male genetic relatedness, group size, and group sex ratio. First, we constructed 2 generalized linear mixed models (GLMM) with a binomial error distribution and logit link function using “lme4” in R v.3.2.1 (R Development Core Team 2017). The binary response variable was extrapair paternity (whether a male group member sired extrapair offspring within his social group or not). In each model, we included the pairwise genetic relatedness between each male group member and male breeder (model 1) or female breeder (model 2), social group size (excluding the breeding pair), and the sex ratio of group members as fixed effects standardized to have sample mean = 0 and sample variance = 1, and group identity as a random effect (model 1: n = 71 group members, n = 23 groups; model 2: n = 61 group members, n = 21 groups). We then conducted a Fisher’s Exact test to examine whether the presence of extrapair offspring in a nest depended on whether the group contained a male that was related to the male breeder (full sibling) (model 3: n = 23 groups).

RESULTS

Group composition and relatedness

Social group size ranged from 3 to 16 adults, with a median size of 8 (mean ± SD = 7.8 ± 3.4; n = 30 groups). Seven breeding pairs were banded at nests found in remote areas of study plots and, because breeding pairs separate from the group while breeding, were not sufficiently resighted postbreeding to identify all members of their group. Social group composition was stable within a breeding season. Most social groups included a socially monogamous breeding pair and group members of both sexes. In 3 groups, we observed plural breeding; 2 breeding pairs attending simultaneously active nests that were clearly from the same social group based on repeated observations of both breeding pairs associating with the same group members. Brood size ranged from one to 3 offspring, with a mode of 3 (mean ± SD = 2.46 ± 0.60; n = 56 broods). The sex ratio (male: female) did not differ from parity for adults in social groups (mean ± SE = 0.51 ± 0.00; n = 28 groups; z = 0.33, P = 0.74) or for offspring in broods (mean ± SE = 0.48 ± 0.01; n = 32 broods; z = −0.37, P = 0.71).

Pairwise relatedness estimates for first-order relatives (mother/offspring, father/offspring, and full sibling relationship dyads identified from parentage analyses) averaged 0.51 (± 0.01 SE; n = 157 dyads) and averaged 0.35 (± 0.03 SE; n = 82 dyads) for second-order relatives (half siblings). However, group members were, on average, unrelated to female or male breeders (0.07 ± 0.02; n = 266 dyads). Paired female and male breeders were unrelated (0.05 ± 0.06; n = 22 dyads; Figure 1).

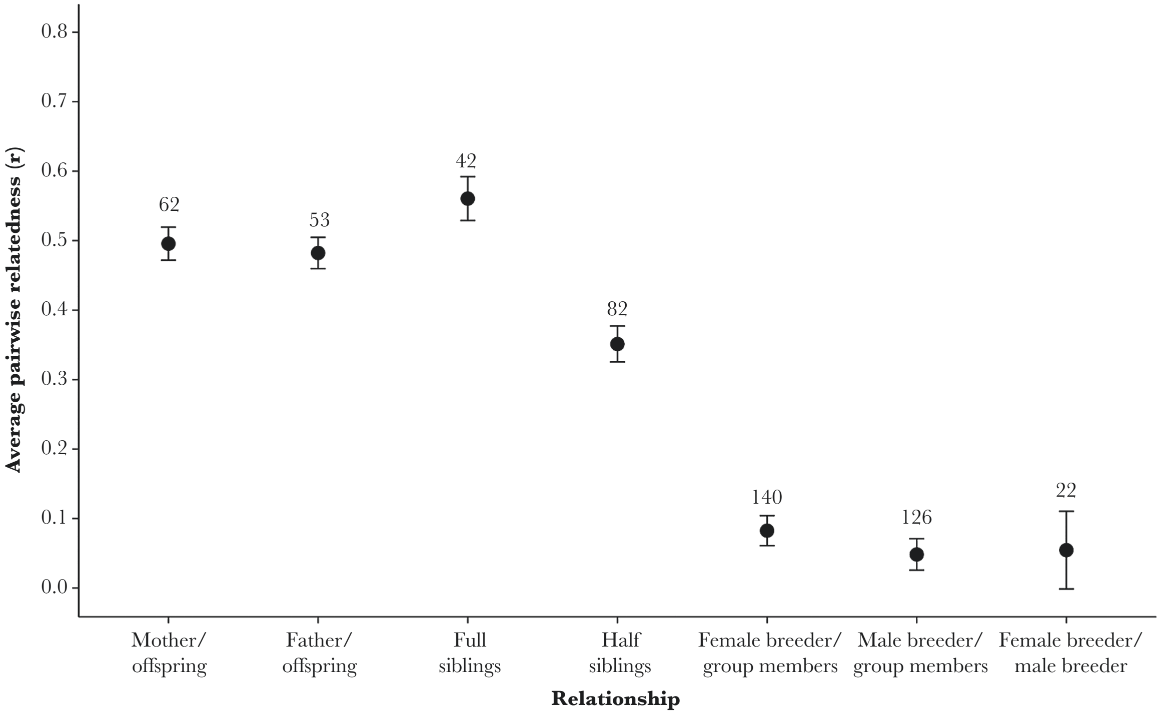

Figure 1
Average pairwise genetic relatedness estimates of gray-throated babblers for first-order relative dyads, including mother/offspring, father/offspring, and full siblings, and second-order relative dyads, including half siblings, female breeders/female group members, male breeders/male group members, and breeding pairs (female breeder/male breeder). Relatedness estimates are given as the coefficient of relatedness (r) ± SE. Sample sizes refer to the number of dyads in each relationship category and are given above each point.

Although most group members were unrelated to the breeding pair, we documented some first-order and second-order relatives of one or both members of the breeding pair (Figure 2). We found that 33 of 140 female breeder/group member dyads (24%) were significantly related (0.36 ± 0.03) and 18 of 126 male breeder/group member dyads (14%) were significantly related (0.40 ± 0.03). Seven of 115 (6%) group members were first-order relatives of both members of the breeding pair (female breeder: 0.41 ± 0.06, male breeder: 0.38 ± 0.04), suggesting that these individuals were within-pair offspring from previous broods that had not yet dispersed from their natal group. However, we were unable to distinguish the relationship between related group members of the female or male breeder because pairwise relatedness estimates fell between first-order (r = 0.25) and second-order relatives (r = 0.50). Group members that were only related to one breeder were not more likely to be relatives of the same-sex breeder than to the opposite sex breeder (chi-square test; female group members: $X_1^2 = 1.38$, $P = 0.24$; male group members: $X_1^2 = 2.08$, $P = 0.15$).

Parental activity

We monitored each nest for an average of 6 h during both the incubation (mean ± SE: 5.91 ± 0.14 h, n = 72) and nestling (mean ± SE: 5.97 ± 0.10 h, n = 85) stages. Two adults (breeding pair) cared for offspring at most nests and shared all parental care duties (nest building, incubation, brooding, and parental provisioning). Group members were not observed incubating in 662 h of videorecording (n = 72 nests), but a third individual sometimes aided with parental provisioning (observed at 9% of 67 nests where the color bands of adults could be identified in 1231 h of videorecordings) and, more rarely (2 of 67 nests), with brooding of nestlings. Mean provisioning rates of helpers were 61% lower than the mean feeding rate of the breeders (mean ± SE: 4.30 ± 0.14 feeding trips hour^{-1}, n = 165 individuals).

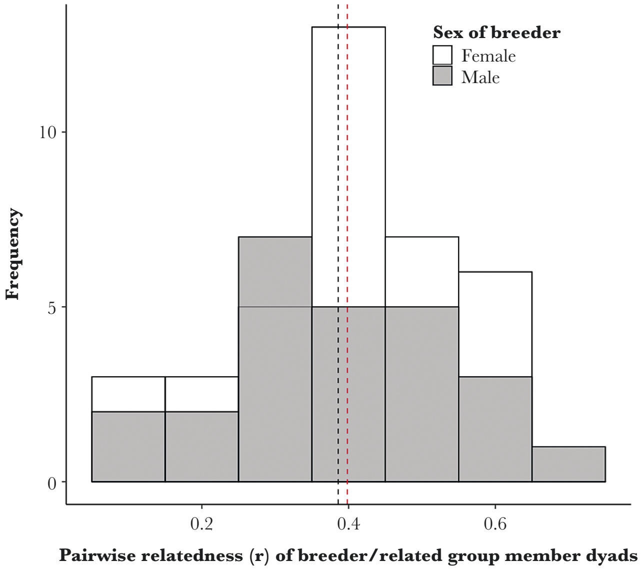

Figure 2
Histogram of the pairwise genetic relatedness estimates of group members that were related to the female breeder (white bars) and/or the male breeder (gray bars) in gray-throated babbler social groups. We only included dyads with group members that were significantly related to the female breeder, male breeder, or both. The average pairwise genetic relatedness estimates are given for the male breeder (black dashed line) and female breeder (red dashed line).

Parentage and kinship assignment

For 31 broods with sampled social mothers, we assigned maternity to 74 of 77 (96%) genotyped offspring using CERVUS. We assigned 71 (96%) offspring to the social mother at the 95% confidence level (≤1 mismatch, positive LOD score). We assigned 3 (4%) offspring of one brood to an unrelated female in the social group that was socially paired with the male breeder in a previous breeding season, although we observed only the social parents visiting the nest to incubate and feed nestlings. The 3 unassigned offspring were from the same brood, and maternity analyses produced ≥2 genetic mismatches with the social mother. In this case, the genetic mismatches could have resulted from genotyping errors or from misidentification of the social mother. However, it is also possible that these offspring were the result of complete brood parasitism by an unidentified extra-group female.

For 6 broods, the social mother was not identified and/or sampled. For 2 broods lacking observations of a female at the nest, but with complete sampling of group members, we assigned entire broods to a single female in each social group (n = 5 offspring). For 7 offspring from 4 broods, we observed a banded, but unsampled female at the nest and maternity analyses produced no genetic matches with other sampled females in the social group. Thus, we had little evidence for conspecific brood parasitism by within-group or extra-group females (i.e., offspring unrelated to the female breeder) or for quasi-parasitism, in which a female lays an egg in another female's nest fertilized by the male breeder at the parasitized nest, Griffith et al. 2004).

For 29 broods with sampled social fathers, we assigned paternity to 67 of 73 (92%) genotyped offspring using CERVUS at the 95% confidence level (≤1 mismatch, positive LOD score). The social father sired 55 (82%) offspring and 10 (15%) offspring were assigned to an extrapair male in the social group. We considered 2 offspring to be sired by an extra-group male because they mismatched their social father and all males in the social group. For the 6 unassigned offspring, we were unable to determine if a male from within or outside of the social group sired them because at least one male within the group was not sampled. Based on the 29 broods with sampled social fathers, the paternity analyses revealed that 18 of 73 (25%) offspring were sired by an extrapair or extra-group male and 10 of 29 (34%) nests contained at least one nestling sired by an extrapair or extra-group male (4 of 10 nests were completely cuckolded; Figure 3).

For 6 broods, the social father was not identified and/or sampled. For one brood lacking observations of a male at the nest, but with complete sampling of group members, we assigned the entire brood to a male in the social group (n = 3 offspring). For 13 offspring from 5 broods, we observed a banded, but unsampled, male at the nest and paternity analyses produced no genetic matches with other sampled males in the social group.

Of 65 genotyped nestlings from 28 broods with unsampled social parents or only sampled social mothers (52 offspring dyads), we found that 29 (56%) offspring dyads were full siblings (r: 0.53 ± 0.03) and 23 (44%) were half siblings (r: 0.25 ± 0.04, extrapair or extra-group offspring) using KINGROUP. However, only 18 (64%) of the full sibling dyads and 10 of the half sibling dyads (36%) were supported by sibling reconstruction in COLONY. This estimate is comparable to the CERVUS estimate of 25% of offspring with known parental genotypes sired by extrapair or extra-group males.

The probability that a male sired extrapair offspring was not influenced by their relatedness to the male breeder (model 1:

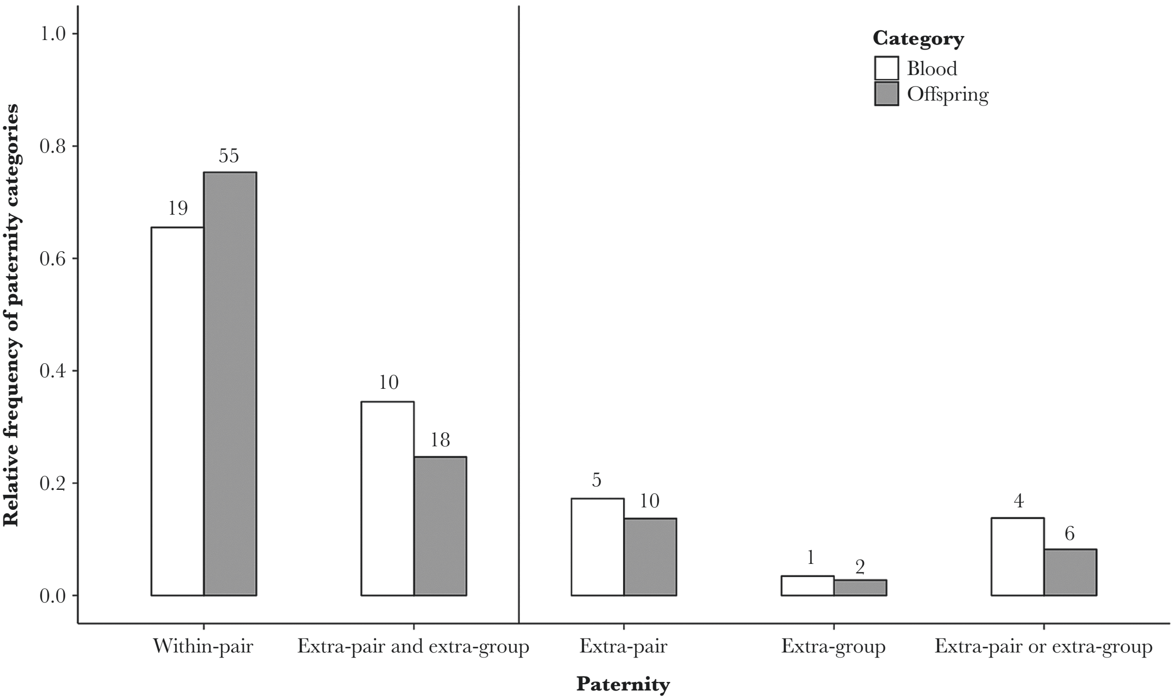

Figure 3

The relative frequency of within-pair paternity, extrapair paternity, and extra-group paternity among broods (n = 29) and offspring (n = 73) in the gray-throated babbler. The vertical line separates the breakdown of the "extrapair and extra-group paternity" category into extrapair paternity, extra-group paternity, and extrapair or extra-group paternity (for offspring that we were unable to assign to a male from within or outside of the group and broods containing these unassigned offspring). Sample sizes refer to the number of broods or offspring for each paternity category and are given above each bar.

GLMM; relatedness: $\beta \pm SE = 0.02 \pm 0.49$, $z = 0.04$, $P = 0.97$) or the sex ratio of the group members ($\beta \pm SE = 0.09 \pm 0.38$, $z = 0.23$, $P = 0.82$). Likewise, this probability was not influenced by their relatedness to the female breeder (model 2: GLMM; relatedness: $\beta \pm SE = 0.31 \pm 0.55$, $z = 0.57$, $P = 0.57$). However, male group members were more likely to gain paternity with decreasing group size (relatedness: $\beta \pm SE = -1.07 \pm 0.53$, $z = -2.04$, $P = 0.041$). Moreover, the presence of extrapair offspring in a nest was independent of whether the social group contained a male sibling of the male breeder (model 3: Fisher's Exact test; $P = 0.66$, $n = 23$ groups).

DISCUSSION

Over the last decade, molecular studies of group living in vertebrates have expanded to reveal remarkable diversity in the structure and composition of social groups in previously underrepresented habitats, geographic regions, and taxa (Cockburn 2004; Lukas and Clutton-Brock 2012; Koenig and Dickinson 2016; Taborsky 2016). However, the Old World tropics remain disproportionately less studied than other regions, even relative to tropical regions in the Western Hemisphere. Here, we characterized the genetic mating system and social structure of an unusual type of group living in an Old World tropical bird wherein nonbreeding conspecifics associate together with one or more breeding pairs and forage as a cohesive group. We found that social foraging groups of the Southeast Asian gray-throated babbler are typically composed of one or 2 socially monogamous breeding pairs accompanied by mostly (80%) unrelated nonbreeding individuals and some (20%) first-order relatives of one or both members of the breeding pair that rarely help at the nest (9% of 67 breeding pairs had a third helper). The "access to mates" hypothesis proposes that in cooperatively breeding species, group members benefit from helping nonrelatives at the nest because they gain direct access to reproduction (Cockburn 1998). We extended this hypothesis to this group-living species with unrelated group members that largely did not help with breeding. Parentage analyses revealed that females did not gain direct access to breeding through brood parasitism, whereas nonbreeding male group members gained direct fitness benefits through extrapair and extra-group paternity (25% of offspring, 34% of broods). These findings fit with the "access to mates" hypothesis in a broader social context and broaden the direct fitness benefits of social foraging for unrelated group members beyond assumed survival benefits.

Reproductive sharing occurs most often in kin-based groups or groups established by coalitions of unrelated males (Riehl 2013). In kin-based groups, male breeders gain inclusive fitness benefits from offspring sired by relatives (Hamilton 1964). In groups containing coalitions of unrelated males (e.g., Henderson's reed warbler, *Acrocephalus vaughani taiti*, Brooke and Hartley 1995) or groups containing unrelated immigrant males (e.g., carrion crow, *Corvus corone*, Baglione et al. 2002), male breeders may share paternity with group members when the fitness costs of losing parentage does not exceed the benefits of cooperation (Emlen 1996; Magrath and Heinsohn 2000; Magrath et al. 2004). We found that similar proportions of nonrelatives and relatives of the male and female breeder were successful at gaining extrapair paternity, suggesting that indirect benefits were not paramount for reproductive sharing.

Reproductive competition among males may also result in cuckoldry of the male breeder if individuals join groups to gain direct fitness benefits, such as increased survival through efficient foraging and coordinated vigilance in large, stable groups (Cockburn 1998;

Kokko et al. 2001; Griesser et al. 2006; Griesser 2013). Larger groups provide more protection from predators than smaller groups (Clutton-Brock 2002; Clutton-Brock 2009). Thus, the male breeder should provide reproductive concessions in small groups in which more incentives are needed for group members to stay than in large groups (Kokko et al. 2001; Kingma et al. 2014). Consistent with this hypothesis, we found that male group members were more likely to gain paternity with decreasing group size. Given that large social groups reduced possibilities for paternity, their benefit likely manifests through increased survival. However, this study was not designed to directly test this possibility. A full evaluation will require examining the trade-offs between the effects of increasing group size on individual survival and on reproductive gains of group members.

The extent of extrapair paternity among group-living species remains unclear and has centered on cooperative breeders. Detailed parentage studies of species that cooperate with nonrelatives remain relatively scarce compared to studies of species that cooperate based on kinship (Dickinson and Koenig 2016; Taborsky 2016). Monogamy has been hypothesized to be less important in the evolution of cooperative breeding in vertebrates because the direct benefits of cooperation do not necessarily depend on kinship (Boomsma 2007). Extrapair paternity in cooperatively breeding species generally increases as the genetic relatedness between male group members and the dominant male breeder decreases (Cornwallis et al. 2010). This would predict higher rates of extrapair paternity in species with nonkin or mixed-kinship groups relative to kin groups. Furthermore, extrapair paternity has mostly been found to occur at low levels or not at all in species that cooperate in kin groups (e.g., red-cockaded woodpeckers (0%), *Picoides borealis*, Haig et al. 1994; bicolored wrens (2.3%), *Campylorhynchus griseus*, Haydock et al. 1996; western bluebirds (0%), *Sialia mexicana*, Dickinson and Akre 1998; American crow (6.9%), *Corvus brachyrhynchos*, Townsend et al. 2009). However, several species of cooperatively breeding Australian fairy-wrens with kin groups have been shown to have high rates of extrapair paternity (Double and Cockburn 2000; Webster et al. 2008). A comparative analysis of the prevalence and levels of extrapair paternity among group-living species with different social structures will require more parentage studies of species that group with unrelated individuals.

An additional path to direct reproduction for male group members is access to extrapair copulations outside of the social group. Gray-throated babblers are not strictly territorial and when social groups encounter each other, they will temporally join each other, which could increase opportunities for extra-group paternity. However, we detected a very low rate of extra-group paternity (<3% of offspring in 4% of broods). Although, this rate might be marginally higher because in a few cases we were unable to identify the extrapair sire as a male from within or outside of the group (6 offspring from 4 broods). Studies of both facultative and obligate cooperative breeders have generally found that extra-group paternity is rare (Appendix 1: Griffith et al. 2002). The most notable exceptions are the superb fairy-wren, *Malurus cyaneus*, and Australian magpie, *Gymnorhina tibicen*, which have the highest recorded rates of extra-group paternity (61% of offspring, Cockburn et al. 2016; 82% of offspring, Hughes et al. 2003, respectively). In these kin-based cooperative breeding systems, extra-group paternity provides the opportunity for males to obtain direct fitness when breeding is constrained because of incest avoidance (Cockburn et al. 2003; Durrant and Hughes 2005). The possibility for incestuous mating is minor in gray-throated babbler groups because of the low genetic relatedness among group members and breeding pairs. Thus, the selection pressure on males to copulate with females outside of the group may be low in the gray-throated babbler and other group-living species with similar group composition and level of genetic relatedness. Taken together, extra-group paternity does not appear to be a primary benefit favoring sociality in this species.

In contrast to parentage gained by some males within social groups, our maternity analyses showed that females did not gain direct parentage within their social group through joint-female nesting or through conspecific brood parasitism. Few cases of brood parasitism have been found in group-living birds (Stacey and Koenig 1990; Koenig and Dickinson 2004, 2016; but see Richardson et al. 2002; Riehl 2010). Conspecific brood parasitism is more often associated with joint-female nesting and is hypothesized to be an evolutionary precursor of joint-female nesting (Vehrencamp 2000). Joint-female nesting has only been documented in species with male-biased incubation leading to strong selection pressure on males to attract additional mates and on females to exploit male parental care (Vehrencamp 2000); male-biased incubation was not observed in the gray-throated babbler. We did document 3 surprising cases of plural breeding, which is generally more common when female group members are related (Keller and Reeve 1994), unlike in the gray-throated babbler. However, the few reproductive benefits gained by females in year-round social groups suggests that other traditional explanations for group-living, such as increased survival, may be the primary benefit of group membership for females.

Our paternity results conflict with 2 long-standing hypotheses. First, the finding that 34% of gray-throated babbler broods contained offspring sired by an extrapair or extra-group male is a notably high rate for a tropical bird, which are predicted to have lower rates of extrapair paternity relative to temperate species because of differences in ecology and life-history traits (Griffith et al. 2002; Macedo et al. 2008). However, few studies of tropical birds have examined extrapair paternity to conduct this comparison and these studies are biased toward the New World tropical regions (Macedo et al. 2008; Tori et al. 2008). Moreover, these studies show high variation among tropical species in extrapair paternity (0–67% of broods; reviewed in Tarwater et al. 2013). Second, species with low adult mortality, such as the gray-throated babbler (21%, Martin, Oteyza, Boyce, et al. 2015), are predicted to have low rates of extrapair paternity (Arnold and Owens 2002). Our study highlights the need for data from more tropical species and social systems, and especially from the Old World tropics, to determine the ecological factors, social (e.g., cooperation) factors, and life-history traits that influence extrapair paternity.

The gray-throated babbler's genetic mating system and social group structure—mostly nonrelatives that assist minimally in breeding—provides an opportunity to test hypotheses about the evolution of social foraging groups in the Old World tropics. High rates of adult mortality, promiscuous mating, or conspecific brood parasitism are hypothesized to give rise to social groups with low genetic relatedness (reviewed in Riehl 2013). However, adult mortality does not explain the low genetic relatedness in the gray-throated babbler because adult mortality is low (Martin, Oteyza, Boyce, et al. 2015) even compared to many other tropical songbirds (Martin 2015; Martin, Oteyza, Mitchell, et al. 2015). Moreover, we show that this species has moderate rates of extrapair and extra-group paternity, and we found little evidence for brood parasitism. Alternatively, groups with low genetic relatedness may have been formed by individuals that joined unrelated breeding pairs or social groups (Riehl

2013), possibly dispersing together with same-sex siblings (e.g., Kalahari meerkat, *Suricata suricatta*, Kutsukake and Clutton-Brock 2008; Arabian babbler, *Turdoides squamiceps*, Ridley 2012). To identify recent dispersers and current levels of dispersal in this gray-throated babbler population, future work will combine estimates of dispersal from mark-recapture data and an assessment of the local genetic structure and centers of kinship. Identifying dispersal patterns will advance our understanding of the factors generating the composition of social foraging groups and the genetic relatedness of group members.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Kaiser et al. (2017).

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