Special Issue: Breeding Aggregations

Home field advantage, not group size, predicts outcomes of intergroup conflicts in a social bird

Meghan J. Strong [a], Benjamin L. Sherman [b], Christina Riehl [a, *]

[a] Princeton University, Department of Ecology and Evolutionary Biology, Princeton, NJ, U.S.A.
[b] 24202 Cornerstone Drive, Yardley, PA, U.S.A.

ARTICLE INFO

Research on cooperatively breeding birds usually focuses on social dynamics within the breeding group, but conflict between groups can also affect individual fitness and the evolution of sociality. Here we investigate the causes and consequences of competition between groups of communally breeding greater anis, *Crotophaga major*, over a 10-year field study. Social groups were spatially clustered into loose aggregations that showed a moderate degree of reproductive synchrony. However, competition between neighbouring groups for nesting sites was intense, occasionally leading to wholesale destruction of a group's nesting attempt and abandonment of the site. We documented 18 cases in which a group's entire clutch of eggs was ejected from the nest during the laying or incubation period, often accompanied by behavioural observations of conflict with a neighbouring group. Clutch destruction typically occurred when two groups attempted to nest in close proximity on high-quality sites: nearest-neighbour distance and nest site type were the strongest predictors of clutch destruction. Surprisingly, group size did not predict whether or not a group's clutch would be destroyed, and small groups sometimes ousted larger groups. By contrast, 'home field advantage' did have a significant effect: groups that had previously nested on the site were more likely to destroy the clutches of newly established groups, and this effect increased with the number of years that the group had nested there. Together, these results support previous evidence that competition between groups for high-quality nesting sites is an important driver of communal breeding, and they highlight the importance of location and past history in determining the outcome of intergroup contests in social species.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

When social groups of animals compete over resources — food, water, mating opportunities, or breeding and foraging territories — larger groups frequently win (reviewed in Lamprecht, 1978; Snaith & Chapman, 2007). This correlation between competitive ability and group size is thought to be an important selective pressure favouring the evolution of sociality (Mosser & Packer, 2009; Pulliam & Caraco, 1984; Wrangham, 1980). However, group size does not always predict the outcome of competitive contests (Harris, 2010), and factors such as group stability, the age and experience of its members and the perceived value of the resource can be equally important determinants of competitive ability (Arseneau-Robar, Taucher, Schnider, van Schaik, & Willems, 2017; Batchelor & Briffa, 2011; Cassidy, MacNulty, Stahler, Smith, & Mech, 2015; Cheney, 1981; Wrangham, 1999).

The majority of studies on intergroup conflicts have focused on social mammals, primarily primates and carnivores, in which groups cooperatively defend their foraging territories against neighbours. Neighbouring groups often interact repeatedly over time, allowing investigation of the relative importance of location, group size and individual participation in determining contest outcome. In white-faced capuchins, *Cebus capuchinus*, for example, Crofoot, Gilby, Wikelski, and Kays (2008) found that group size did confer a competitive advantage, but that this advantage was far more important at the periphery of a group's territory (where the costs of losing were relatively small) than near the centre (where the costs of losing were presumably larger). Similar interactive effects of location and group size have subsequently been documented in banded mongooses, *Mungos mungo* (Furrer, Solomon, Willems, Cant, & Manser, 2011), black-and-white colobus monkeys, *Colobus guereza* (Harris, 2010), baboons (*Papio cynocephalus*; Markham, Alberts, & Altmann, 2012), blue monkeys, *Cercopithecus mitis* (Roth & Cords, 2016), and chimpanzees, *Pan troglodytes* (Wilson, Kahlenberg, Wells, & Wrangham, 2012).

* Correspondence: C. Riehl, Princeton University, Department of Ecology and Evolutionary Biology, Princeton, NJ 08544, U.S.A.
    E-mail address: criehl@princeton.edu (C. Riehl).

Much less is known about the factors influencing the outcome of intergroup contests in social birds, or even about the fitness costs of these contests. Research on cooperatively breeding birds has largely focused on conflicts of interest within the social group rather than between groups (reviewed in Koenig & Dickinson, 2004). However, intergroup competition can also influence individual fitness, since cooperative groups often defend foraging territories, breeding sites or all-purpose territories that are used for both nesting and foraging (Golabek, Ridley, & Radford, 2012). It has long been hypothesized that competition over limited nest sites is an important driver of the evolution of cooperative breeding (Emlen, 1982; Gaston, 1978), but few studies have examined the relative importance of group size and other group-level traits in determining the odds of success. Radford and du Plessis (2004) found that cooperative groups of green woodhoopoes, *Phoeniculus purpureus*, compete for territories by performing cooperative calling displays: during short contests, residents tended to oust intruders, but during long contests, residents gained no advantage and group size was correlated with success. In subdesert mesites, *Monias benschi*, which also sing communally when encountering neighbouring groups, Seddon and Tobias (2003) found that resident groups were more likely to respond to playbacks of simulated 'intruder' groups if the resident group outnumbered the intruders. This suggests both that group size influences the outcome of territorial interactions and that communal vocalizations convey information about the size of the singing group.

In this study, we investigated intergroup conflicts in the greater ani, *C. major* (hereafter 'ani'), a cooperatively breeding Neotropical bird, to identify characteristics that influence competitive ability. Ani nesting groups typically consist of either two or three pairs that all reproduce in a shared nest; about 15% of groups also include an unpaired, nonreproductive helper. Group size therefore ranges from four to seven birds, with lone pairs and larger groups occurring very rarely (Riehl & Jara, 2009; Riehl, 2011). Reproduction is divided roughly equally among the group's breeding pairs, and all group members participate in nest building, provisioning and defence of the communal clutch (Riehl, 2011, 2012). Ani groups do not appear to defend a defined foraging territory — individuals range widely while foraging, often overlapping the foraging areas of neighbouring groups — but they aggressively defend the nest site itself by chasing extragroup individuals and by performing loud, stereotyped communal chorusing displays (Riehl & Jara, 2009). Like many Neotropical birds, adults are long-lived (≤ 20 years), sedentary and remain on their breeding territories year-round. Groups vary in stability; some groups remain together on the same site for over a decade, while others experience high turnover in composition or abandon the nesting site after 1—3 years (Riehl & Strong, n.d.)

Previous studies on our long-term study population in Panama have shown that anis nest exclusively along the shores of lakes and rivers, either in tree branches overhanging the water's edge or in emergent bushes or small trees that are surrounded by water (Riehl & Jara, 2009; Riehl, 2011). Nests built in emergent vegetation experience substantially lower rates of nest predation than do nests built along the shoreline, apparently because they are less vulnerable to terrestrial predators such as snakes and monkeys (Lau, Bosque, & Strahl, 1998; Riehl, 2011). Large groups are more likely to acquire and defend these high-quality, emergent nest sites than are smaller groups (Riehl, 2011), suggesting that these sites are limited and that competition between groups is at least partly influenced by group size. Consistent with this hypothesis, each group vigorously defends the immediate nesting area from extragroup individuals, often chasing members of neighbouring groups or unattached 'floaters' away from the nest. Ani groups also forage near their territories, but do not defend these larger foraging areas.

Nest site 'quality', therefore, is defined in terms of its accessibility to predators, not by the food resources available at that site.

Intergroup interactions most frequently take the form of communal chorusing displays, in which group members gather in a circular huddle and collectively give a mechanical 'gurgling' call that may last up to 10 min and is given only in the context of group displays (Riehl & Jara, 2009). These displays occur several times per day, typically in the vicinity of the nest, and are often given in response to displays by neighbouring groups. Intergroup conflicts can also escalate to chasing and physical aggression (typically followed by communal displays), especially when an extragroup individual approaches the nest.

In this study, we describe a rare but costly type of intergroup conflict: destruction of a nesting group's communal clutch of eggs, resulting in failure of the nesting attempt and abandonment of the territory. In these instances, all of the eggs in a group's communal clutch were found underneath the nest, intact, apparently having been ejected by extragroup conspecifics. We hypothesized that wholesale clutch destruction is a result of competition between neighbouring groups for high-quality nest sites, and we predicted that nest site quality, density of groups and distance between nearest neighbours would influence the risk of conflict. Because clutch destruction is rare in the study area and was never observed directly, we tested these predictions indirectly by identifying spatial and ecological correlates of clutch destruction. First, we analysed the spatial distribution of ani breeding groups across the study area to determine whether nesting groups are spatially aggregated and/or reproductively synchronized, since groups that are clustered in space and time are more likely to experience competition over nest sites and resources. We then constructed statistical models to identify factors influencing the likelihood of clutch destruction. Finally, we compared group size and nest site tenure (number of years on the nest site) of groups whose clutches were destroyed with those of their nearest neighbours — the apparent aggressors.

METHODS

Study Species and Data Collection

We collected long-term data from a nesting population of greater anis in the Barro Colorado Nature Monument, Panama (9°9′16″N, 79°50′44″W), during 2007—2016. Most (~70%) breeding groups in the study population consist of two pairs, ~25% consist of three pairs and <5% consist of four or more breeding pairs (Riehl, 2011). Each group constructs a single nest in which all of the breeding females lay their eggs. One type of egg destruction occurs in a highly stereotyped pattern at communal nests and is performed by group members, not by extragroup individuals. Prior to laying her own first egg, each female removes any eggs that other females in the group have already laid in the shared nest. After a female lays her own first egg, she stops removing eggs from the nest, presumably in order to avoid removing her own eggs. As a result, the first female to begin laying always loses at least one egg (sometimes several), and the last female to enter the laying sequence loses none, a pattern observed in both greater and groove-billed anis, *Crotophaga sulcirostris* (Riehl & Jara, 2009; Vehrencamp, 1977). Once all of the females in the social group have begun to lay, eggs accumulate in the communal nest in a predictable pattern (each female lays one egg every other day) and egg ejection by group members is no longer observed (Riehl, 2010a). Each female in the social group contributes three to four eggs to the final clutch; total clutch size is therefore between six and 15 eggs, depending on the number of females in the group. Because the patterns and costs of within-group egg ejection are

already well understood (Riehl, 2011; Vehrencamp, 1977), this study focuses on intergroup rather than within-group dynamics.

Between 40 and 60 communal ani nests were located and monitored yearly. Ani groups typically build a complete nest at the beginning of the nesting season (mid-July), which they defend through the reproductive period (early September); laying may occur weeks to months after nest construction. Since we were primarily concerned with understanding the factors leading to clutch destruction in this study, we defined the initiation date of the nesting attempt as the first day on which the first egg was laid in the communal nest, and the termination date as the last day on which an egg was present in the communal nest. Nests were checked daily prior to laying and during laying, every 2–3 days during the 12-day incubation period, daily during the first 6 days of the nestling period, and every 2–3 days thereafter until the nestlings fledged or disappeared. Eggs were individually numbered in the order in which they were laid with a permanent, nontoxic felt-tipped marker and the fate of each egg was recorded (ejected, depredated, or hatched). At each visit to the nest, observers noted the number of adults participating in communal displays; this measure is highly repeatable and is an accurate count of absolute group size (Riehl, 2011). The number of reproductive pairs per group was also verified by the timing of laying in the communal nest and by genetic identification of egg maternity and nestling parentage. Finally, observers opportunistically noted behavioural evidence of intergroup conflicts during nest checks (instances where individuals from one group were directly observed chasing or giving alarm calls at members of a neighbouring group, and/or performing communal displays in response to the presence of a neighbouring group).

The eventual fate of each nest was recorded as successful (fledged offspring) or unsuccessful (did not fledge offspring), and the cause of nest failure was recorded as either intergroup clutch destruction or any other fate (including predation, failure due to weather, or unknown causes). Predation and egg ejection were typically easy to tell apart in the field, since eggs were found immediately underneath the nest in the latter. It was more difficult to distinguish between cases of intragroup egg ejection (which occur at virtually all communal nests, as described above) and cases of intergroup egg ejection (which were rare). We primarily used differences in timing and laying patterns: egg ejection within the social group is restricted to the beginning of the laying cycle, typically occurs immediately after each egg is laid and ceases when all of the group's females have started to lay (Riehl & Jara, 2009; Riehl, 2010a). By contrast, egg ejection by extragroup individuals occurs at various points in the laying and incubation periods and after all of the group's females have laid eggs in the nest. Laying activity by group members was confirmed by genetic analysis.

Genetic Sampling and Analyses

Maternal DNA was collected noninvasively from the surface of freshly laid eggs using protocols described by Schmaltz, Somers, Sharma, and Quinn, 2006 and modified and validated for this study population (Riehl, 2010b). Briefly, the surface of the shell was swabbed with a Q-tip (concentrating on areas with visible maternal blood stains) within 24 h of laying, and the head of the Q-tip was stored in lysis buffer. DNA from eggshell swabs was extracted using Omega E.Z.N.A. Forensic DNA spin columns (Omega Bio-Tek Inc., Norcross, GA, U.S.A., catalogue no. D3591) and eluted in 200 μl elution buffer to maximize total yield. These initial elutions typically exhibited low DNA concentration (<6 ng/μl) and high levels of impurities, and were subsequently cleaned and eluted in smaller volumes using Agencourt AMPure XP magnetic beads (Agencourt Bioscience, Beverly, MA, U.S.A., catalogue no. A63881; final target

concentration >30 ng/μl). Maternal DNA was also destructively sampled from the shell membranes of ejected, nonincubated eggs using protocols described in Strausberger and Ashley (2001). Omega E.Z.N.A. Forensic DNA kits were also used for these extractions, but the AMPure purification/clean-up step was not necessary for successful amplification.

Nestlings were permanently banded with a unique combination of coloured metal leg bands at 4–5 days of age, and blood samples (<10 μl) were taken by brachial venipuncture at 2–3 days of age for genotyping. During 2007–2011, 25–50 breeding adults per year were captured in mist nets, individually colour-banded and bled via brachial venipuncture ($N = 225$). However, the plastic colour bands used for adults in 2007–2011 (Darvic flat bands, wraparound-style; https://www.avinet.com/en/bands/darvic) tended to fade and fall off after ~3 years, so identification of individual group members across years was primarily through genetic analysis of their eggs and nestlings rather than by colour bands. Nestlings, adults and maternal DNA from eggshells were genotyped using a set of 12 highly polymorphic microsatellite markers developed for this species (Almany et al., 2009); the measured typing error rate was 0.7%. Identification of maternal genotypes is straightforward, requiring only comparison of genotypes within the nest to identify unique maternal signatures (Riehl, 2010b). Genetic information from eggs can therefore be used to confirm a female's membership in a group across years, as well as the number and identity of eggs that the female contributes to the communal clutch. Group membership of adult females was therefore determined by a combination of resighting of colour-banded individuals and genetic identification of egg maternity. Group membership of adult males was determined by a combination of resighting of colour-banded individuals and genetic analysis of sibling relationships in a group's clutch across years (for example, if nestlings in a clutch one year were full siblings of nestlings in the group's clutch the same year, we assumed that the same parents were members of the group in both years). We used the program COLONY 2.0 (Jones & Wang, 2010) to partition communal clutches into clusters of full siblings, half siblings, or unrelated nestmates; parentage was assigned using CERVUS 3.0.7 as in Riehl (2012).

We used genetic information from three different sources (egg, nestling and adult samples) in combination with observations of colour-banded individuals to determine group stability and site fidelity across years, as in Riehl (2011). Group stability was measured as the proportion of reproductive adults present in a breeding group in one year that were also present the subsequent year, and the same group was considered to reside on a nesting site for two successive years when at least 75% of the individuals present in the group in one year nested on the same site in the subsequent year. The project began in 2007; therefore, no information on tenure length was available for groups originally located in that year, and only minimum possible tenure lengths were known for groups first located in 2007 and tracked in subsequent years. Minimum possible tenure lengths were therefore used in the analyses for these groups.

Spatial Analysis and Reproductive Synchrony

We used ArcMap 10.3.1 (Environmental Systems Research Institute, ERSI, Redlands, CA, U.S.A.) to calculate pairwise distances between nests, the mean distance between nests and nearest-neighbour distance for each nest in the study area each year. Ani groups occasionally build a second nest and attempt to renest if the first clutch fails; however, the second nest is usually in the same bush or shrub as the first nest (often <1 m from the first nest; Riehl & Strong, n.d.), so when renesting attempts were included in the analyses, the same location was used for both nests. The point

M. J. Strong et al. / Animal Behaviour xxx (2017) 1–9

density tool in ArcMap was then used to measure the density of 'points' (nests) per square kilometre given a predetermined radius around each nest. We used the mean distance between nests for each year, a biologically relevant measurement, as the radius for each nest. This analysis produced a heatmap of the overlap of radii between nesting groups, with warmer colours indicating dense clusters of nesting groups, or neighbourhoods (Fig. 1). To quantify reproductive synchrony among nesting groups, we used Kempenaers's (1993) synchrony index formula (modified from

Björklund & Westman, 1986), which measures the degree of overlap of fertile periods of each female in a breeding population. Values of the synchrony index (SI) range from 0% (no synchrony) to 100% (complete synchrony). In greater ani groups, breeding females in the same nesting group are by necessity in reproductive synchrony, since the communal clutch does not accumulate until all of the group's females have started to lay. Therefore, we calculated synchrony across breeding groups rather than across individual females. Each group thus represents one reproductive unit and
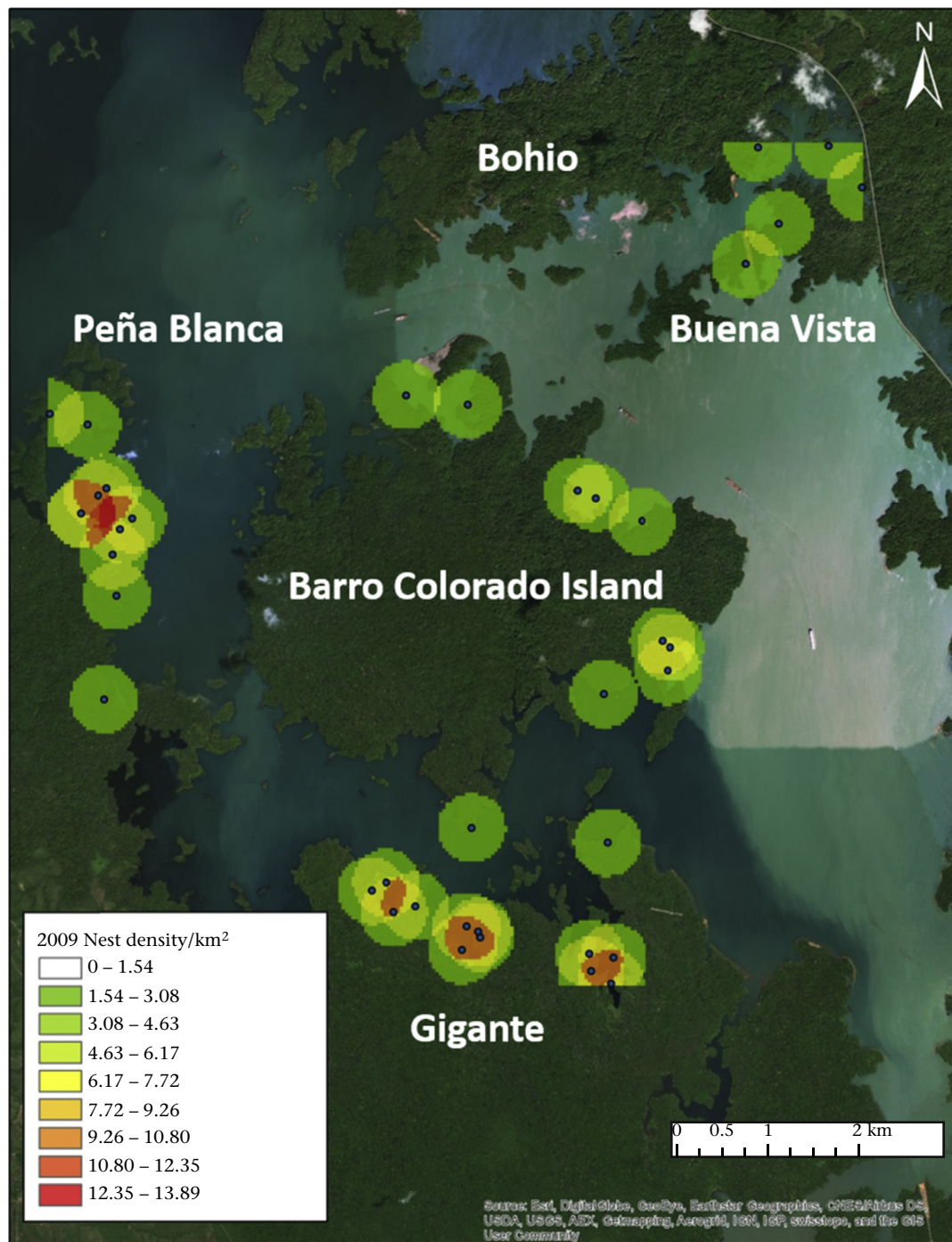

Figure 1. Satellite map of locations of greater ani nests at Barro Colorado Nature Monument, central Panama, showing Barro Colorado Island and mainland peninsulas; 2009 (the fifth peninsula, Frijoles, is not shown). Each dot represents one nest and the radius of each green circle represents the mean distance between nests. Warmer colours indicate higher local density of nesting groups.

synchrony was calculated using the laying dates of the first and the last egg of each group. We developed a program in LabVIEW (National Instruments Corporation, Austin, TX, U.S.A.) to calculate synchrony indices for the entire study area each year and for each site within the study area (Barro Colorado Island and the mainland peninsulas Frijoles, Bohio, Gigante, Peña Blanca and Buena Vista). Following Marsden and Evans's (2004) modification of Kempenaers's (1993) method, we used a Monte Carlo randomization to simulate the distribution of reproductive synchrony under random expectations, and compared our observed values to the null distribution to identify statistically significant deviations ($P < 0.05$ with Bonferroni correction for multiple hypothesis testing). Because the distributions of synchrony indices across sites and clusters were not normal, we also used Wilcoxon signed-ranks tests to ask whether synchrony indices across sites differed significantly from those under random expectations. Sampling of the study area was restricted in 2010–2011 and focused primarily on groups for which we possessed long-term data, so analyses of nest density and synchrony excluded data from these years.

Statistical Analyses and Sample Sizes

A total of 353 nesting attempts were observed over the study period; for 22 of these, groups built and defended nests, but did not lay eggs. We obtained complete data for egg maternity, initiation and termination date, and nest fate, for 192 of the remaining 331 nesting attempts. We used multilevel mixed-effects logistic regression models to identify factors predicting the probability of a nesting attempt being destroyed by a conspecific group (=1) versus any other fate (=0). 'Any other fate' included nests that were depredated, destroyed due to weather or unknown causes, or successfully fledged. Initial models included all variables of potential biological relevance, including the number of individuals in the nesting group (absolute group size), the local density of nesting groups (measured using the point density function in ArcMap, described above), the linear distance to the nearest neighbouring group, the type of nesting territory (0 = shoreline, 1 = emergent vegetation), the initiation date of the nest (standardized for year by subtracting the initiation date from the mean and dividing by the standard deviation for that year) and the total number of days over which the nest would have been vulnerable to attack by conspecifics (i.e. the total number of days for which eggs were recorded to be present in the nest). Since previous studies have found that larger groups are more likely to nest on high-quality territories, we also included the interaction between absolute group size (number of group members) and nest site type. Finally, group identity was included as a random effect in all models to account for repeated measures, since most groups were sampled across several years.

Best-fit models were selected using a 'best-subsets' approach, in which initial models included all terms and were compared with all possible models using subsets of the terms. Models were evaluated with Akaike's information criterion corrected for finite sample size (AICc; Burnham & Anderson, 2002). Models within two AIC_c units of the top model ($\Delta AIC_c = 0$) were candidates of potential explanatory value; however, models within two AIC_c units of the top model that differed from a higher-ranking model by the addition of one parameter were rejected as uninformative, as recommended by Arnold (2010). Full model results and overall significance tests for models are presented in Supplementary Table S2; inferences from models were made only when the overall model was significant. Analyses were conducted in STATA 14 (StataCorp LP, College Station, TX, U.S.A., http://www.stata.com/stata14/), statistical significance was set at α = 0.05, and results are given as means ± SE unless otherwise reported.

For the nesting groups whose clutches were destroyed by neighbouring groups, we conducted a second set of analyses to compare traits of groups that were attacked with traits of the most likely aggressors, their nearest neighbouring groups. In no instances could we identify the aggressor group with absolute certainty, since clutch destruction was never directly observed; however, both behavioural observations of intergroup conflict and the results of the aforementioned analysis (see Results), indicated that aggressor groups were most likely to be the nearest neighbours of the attacked group. Since we obtained complete information from only 18 pairs of attacked groups and their nearest neighbours, we performed matched-pairs comparisons rather than constructing statistical models. We used Wilcoxon signed-ranks tests to determine whether attacked groups and their nearest neighbours differed in size (number of individuals) or in tenure length (number of years that the group had been present on the nest site).

Ethical Note

Field sampling methods were approved by the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute (protocols numbers 2007-02-03-15-07, 2015-0601-2018). Export permits for genetic material were granted by Panama's Autoridad Nacionál del Ambiente (ANAM), and import permits to the U.S. were granted by the United States Department of Agriculture. DNA sampling of maternal blood from eggs is noninvasive and has had no observable effects on egg viability. During banding and blood sampling, nestlings were held for less than 10 min and the amount of blood taken (<45 μl, 0.05 g) was less than 1% of body mass (minimum nestling body mass = 30 g), well below the recommended limits for avian blood sampling (Voss, Shutler, & Werner, 2010). Nestlings that appeared weak or dehydrated were not bled, and nestlings were taken a short distance away from the nest during processing to minimize stress to the adult group members, who appeared most disturbed when researchers were present at the nest. Nests were accessed by water to avoid damaging vegetation, and all nest checks were kept to a minimum to avoid disturbance. Nests were not approached when potential predators were present, to avoid attracting their attention to the nest (primarily keel-billed toucans, *Ramphastos sulfuratus*, and white-faced capuchins, *C. capuchinus*).

RESULTS

Spatial Clustering and Reproductive Synchrony

Spatial analysis revealed that nesting groups were nonrandomly distributed over the study area, frequently clustering in loose aggregations of up to nine groups/km² (Fig. 1; Supplementary Fig. S1). At the level of the entire study area, nesting groups did not exhibit significant reproductive synchrony across the 3-month breeding season. For the 8 years for which we had sufficient data to analyse reproductive synchrony (2007–2009, 2012–2016), synchrony indices ranged from 13.5% to 47.6% (mean ± SE = 22.1 ± 3.8) and did not deviate significantly from random expectations in any year (Supplementary Table S1). However, nesting groups showed moderate reproductive synchrony at the six sites within the study area (Barro Colorado Island and mainland peninsulas Frijoles, Peña Blanca, Gigante, Bohio and Buena Vista). Reproductive synchrony within sites ranged from 0% to 68% (mean ± SE = 26.5 ± 3.1) and was significantly higher than predicted by Monte Carlo randomization (Wilcoxon signed-ranks test: $Z = 2.3$, $P = 0.02$; Supplementary Table S2).

Occurrence and Predictors of Intergroup Clutch Destruction

Of 192 nesting attempts for which we collected complete data, 18 clutches (9.3%) were apparently destroyed by conspecifics outside the social group. In all cases, eggs were found immediately underneath the nest during either the incubation period ($N = 11$) or the laying period ($N = 7$), after all of the females in the breeding group had started to lay. In the majority of cases ($N = 14$), field observers noted behavioural evidence of conflict between groups whose clutches were destroyed and their nearest neighbours (e.g. chasing, alarm calling and communal displays) immediately before or immediately after the clutch was destroyed. Although we never directly observed clutch destruction in the field, we suspect that eggs were rolled out of the nest by extragroup individuals in much the same manner that within-group females ordinarily use to remove eggs at the beginning of the nesting cycle. In two cases, eggs were found underneath a group's nest over the course of several days, accompanied by behavioural observations of frequent conflicts between the attacked group and their nearest neighbours (including chasing, alarm calling and close approaches to the attacked group's nest). In only one of 18 instances did an attacked group successfully renest and fledge offspring; in the other 17 instances, the group abandoned the territory. Overall, predation accounted for the majority of nest failures ($N = 99$, 51.6%), followed by intergroup clutch destruction ($N = 18$, 9.3%) and weather ($N = 2$, 1.0%). The remaining 73 nesting attempts (38.0%) successfully fledged at least one offspring.

Mixed-effects logistic regression models revealed that clutch destruction was most likely to occur when two groups attempted to nest in close proximity on high-quality nest sites (those on small islands of emergent vegetation). Three competitive models were assigned AICc scores within 2 AICc units of each other. All three included nearest-neighbour distance and nest site type (or the interaction between group size and nest site type) as significant predictors of the likelihood that a clutch would be destroyed (Table 1). Because these models were equally well supported, we performed model averaging (Symonds & Moussalli, 2010) to estimate the effect sizes of each variable (Table 2). Nest site type and nearest-neighbour distance were the only predictors for which 95% confidence intervals did not overlap zero (Table 2). Clutch initiation date and the total number of days that the clutch was vulnerable to attack by conspecific ('total days') were also retained in the top models; however, including local nest density did not significantly improve model fit compared to the top models (Supplementary Table S3). Post hoc analyses confirmed the effects of nearest-neighbour distance and nest site type. Whereas the average distance between nearest neighbours across all dyads in the study area was 478.9 m ($\pm$ 35.9), the average distance between attacked nests and their nearest neighbours was only 257.7 m ($\pm$ 34.6). This difference was significant ($t_{190} = 1.97$, $P = 0.05$; Fig. 2). Nests built on high-quality emergent sites were more likely to be destroyed, with 72.2% of attacked nests and only 20.7% of non-attacked nests built on emergent nest sites ($\chi^2_1 = 22.8$, $P < 0.0001$; Fig. 2).

Table 2
Effect sizes (β), standard errors (SE) and 95% confidence intervals (CI) of explanatory variables for the binary probability of a nesting attempt being destroyed by a conspecific group ($= 1$, $N = 18$) versus any other fate ($= 0$, $N = 174$), obtained from model averaging of the three competitive models presented in Table 1.

Variables	β	SE	95% CI	
Nest site type	2.762	0.263	1.377	4.143
Nearest-neighbour distance (m)	0.854	0.023	0.370	1.215
Nest site type*group size	0.533	0.018	−0.797	0.269
Group size	0.237	0.054	−0.330	0.805
Initiation date	0.001	0.012	0.001	0.001
Total days	−0.018	0.091	−0.091	0.054

Nest site type (1 = emergent vegetation, 0 = shoreline vegetation) was coded as a binary variable, and initiation date was standardized by year.
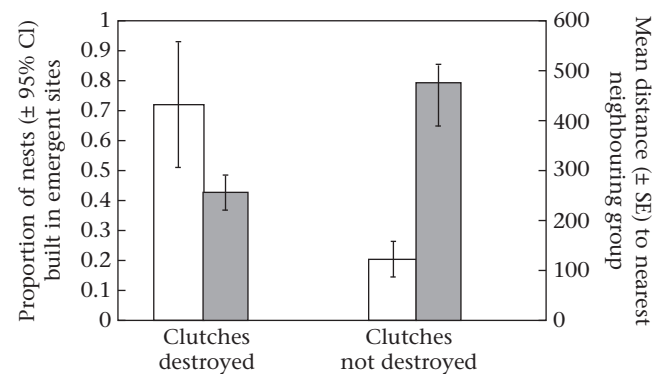

Figure 2. Proportion of nests built on emergent sites (white bars, left axis) and mean nearest-neighbour distance in metres (grey bars, right axis) for clutches destroyed by conspecific nesting groups ($N = 18$) and clutches that were not destroyed by conspecific nesting groups ($N = 143$). Error bars represent 95% confidence intervals and standard errors, respectively.

Effects of Group Size and Prior Experience

To identify group-level characteristics predicting the outcome of intergroup conflicts, we conducted paired comparisons of the 18 groups whose clutches were destroyed with their nearest neighbours (the group that was likely the aggressor). There was no significant difference in absolute group size between attacked groups and aggressor groups (Wilcoxon signed-ranks test: $Z = -0.36$, $P = 0.72$). The mean ($\pm$ SE) size of groups whose clutches were destroyed was 4.78 ± 0.30 individuals (range 4–8), and the mean size of their nearest neighbouring group was 4.56 ± 0.25 individuals (range 4–7). In six cases the attacked group was larger than the aggressor group, in four cases it was smaller, and in eight cases the two groups had the same number of members (Fig. 3a).

However, attacked groups and aggressor groups did differ in the number of years that they had previously nested on the site (tenure length; Wilcoxon signed-ranks test: $Z = -2.12$, $P = 0.005$). For the 15 pairs of nests for which tenure length was known, the mean tenure length of groups whose clutches were destroyed was

Table 1
Mixed-effects logistic regression models within 2 AICc units of the best-fit model, predicting the binary probability of a nesting attempt being destroyed by a conspecific group ($= 1$, $B = 18$) versus any other fate ($= 0$, $N = 174$)

Random effects:	AIC$_c$	ΔAIC$_c$	Model likelihood	AIC$_c$ weight	Evidence ratio
Nest site type, initiation date, total days, nearest-neighbour distance	85.35	0.00	1.00	0.21	1.36
Nest site type*group size, initiation date, total days, nearest-neighbour distance	85.97	0.62	0.73	0.16	1.54
Nest site type, initiation date, nearest-neighbour distance, density	87.01	1.66	0.44	0.09	1.09

Group ID was included as a fixed effect in all models to control for repeated measures across years. Evidence ratios compare each model to the next lowest-ranked model. All models and their ranks are presented in Supplementary Table S3.
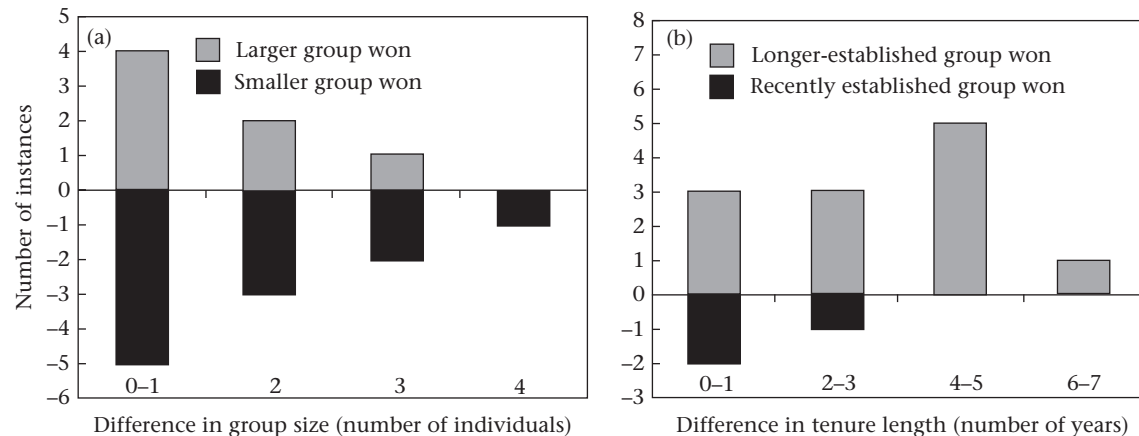
Figure 3. (a). Difference in group size for 18 groups whose clutches were destroyed and their nearest neighbouring group. Grey bars denote instances in which a larger group apparently destroyed the clutch of a smaller group, and black bars indicate instances in which a smaller group apparently destroyed the clutch of a larger group. (b). Difference in tenure length (number of years occupying a nesting territory) for 15 groups of known tenure length whose clutches were destroyed and their nearest neighbouring group. Grey bars denote instances in which a longer-established group apparently destroyed the clutch of a more recently established group, and black bars denote instances in which a more recently established group apparently destroyed the clutch of a longer-established group.

0.67 ± 0.23 years (range 0–2), whereas the mean tenure length of their nearest neighbours was 3.27 ± 0.65 years (range 0–7). In 9 of 15 cases, a previously established group destroyed the clutch of a group that had never before nested at the site; and in 2 of 15 cases, a longer-established group destroyed the clutch of a more recently established group. In the remaining three cases, a more recently established group ousted a longer-established group, and in all three cases the difference in tenure length was ≤ 2 years (Fig. 3b).

DISCUSSION

In this study, we found that greater ani groups often nest at high densities and in spatially aggregated clusters. Rarely, conflicts over nesting territories appear to result in attacks on the nest itself, resulting in eviction of the group's eggs and abandonment of the nest. These conflicts were most likely to occur on small islands of emergent vegetation (sites that are less vulnerable to terrestrial predators), particularly when two groups built nests in close proximity to one another; and usually resulted in eviction of the more recently established group by a longer-established group.

Competition over nest sites is common in birds and often involves destruction of eggs or young, especially in cavity-nesting species for which nest sites are limited. In cliff swallows, *Petrochelidon pyrrhonota*, tree swallows, *Tachycineta bicolor*, house wrens, *Troglodytes aedon*, marsh wrens, *Cistothorus palustris*, woodpeckers and other cavity-nesting species, egg and nestling destruction by conspecifics is relatively common and usually results in nest usurpation by the aggressors (reviewed in Lindell, 1996). These attacks are relatively less common in open-cup nesters, although Heinsohn's (1988) report of intergroup conflict in cooperatively breeding white-winged choughs, *Corcorax melanorhamphos*, is remarkably similar to this study. Like greater anis, white-winged chough groups live in stable social groups that defend an open-cup nest rather than a foraging territory. Over three years, Heinsohn (1988) observed several instances in which members of one group dislodged and destroyed the nests of neighbouring groups (once evicting the eggs and leaving the nest intact); all instances occurred when two groups built nests relatively close to one another (within 500 m).

The evidence in this study suggests that, as in white-winged choughs, the main benefit of intergroup clutch destruction in anis is to indirectly reduce competition over local resources rather than to take over the nest site itself. We never observed an aggressor group laying eggs in the evicted group's nest; rather, in all 18 instances, the presumed aggressor group had already built a nest close by (and in most cases had already laid eggs). Anis have large clutches (up to 11 nestlings), which they feed large arthropods; approximately 8% of nestlings die from starvation, suggesting that resources during the nestling period are limited (Riehl, 2016). Destruction of neighbouring groups' nesting attempts might therefore reduce local competition for arthropods during the period when need is greatest, especially since nests in the same area tend to be reproductively synchronized. We suspect that attacks on neighbouring nests are carried out by single individuals rather than by the entire breeding group, since behavioural observations of conflict usually involve one or two extragroup individuals approaching a group's nest and being chased away by the residents, rather than entire nesting groups engaging in conflict. If so, this may account for the lack of correlation between relative group size and the likelihood of clutch destruction; however, we lack direct observational data to confirm this. In white-winged choughs, nest destruction was also performed by single individuals rather than by the entire group; however, in all but one instance, the attacked group was smaller than the aggressor's group (Heinsohn, 1988).

Macedo, Cariello, and Muniz (2001) suggested an alternative hypothesis for clutch destruction observed in guira cuckoos, *Guira guira*, a close relative of the greater ani that shares a similar breeding system. In guira cuckoos, nestlings are commonly killed and/or ejected from the nest sequentially, often leading to failure of the nesting attempt (Macedo & Melo, 1999). Macedo et al. (2001) suggested that infanticide might be an adaptive strategy to force renesting, possibly creating new reproductive opportunities for either extragroup individuals or group members who did not contribute young to the first nesting attempt. However, this is unlikely to explain clutch destruction in greater anis for several reasons. Greater ani groups are smaller and more stable than guira cuckoo groups: egg ejection by group members is limited to the beginning of the laying cycle, so the number of eggs that each female contributes to the incubated clutch is nearly equal (Riehl, 2011). Therefore, it is unlikely that it would be adaptive for a group member to force renesting after already laying eggs. Second, in no cases did we observe an attacked group successfully renesting: in two cases, an attacked group attempted to lay a second

clutch of eggs after the first was ejected, but in both cases the group was attacked again and the second clutch of eggs was ejected as well. In one of these cases, the attacked group was finally able to renest successfully, but not until 4 months after the breeding season had ended — the only breeding attempt during the dry season that we have recorded in over 10 years. Finally, direct behavioural observations suggest that clutch destruction was preceded by frequent aggression between two closely neighbouring groups, including chasing and alarm calls. In one case where two groups nested within 50 m of one another on a small (<1 ha) island, eggs were ejected sequentially from one clutch during laying and individuals were seen flying between the two nests. Within 1 week, several eggs were ejected from the other nest. All eggs were eventually ejected from both nests, and both were ultimately abandoned. However, despite the circumstantial evidence for the identity of aggressor groups in this study, it is important to note that we could not directly verify which group was the attacker, so our assumption that the nearest neighbouring group was responsible may not have been correct in all cases.

There are several potential explanations of the observed correlation between a group's tenure on the nest site and the likelihood of success in intergroup conflicts. First, the expected payoffs for the conflict may be asymmetrical: a group that has nested on the same territory for several years might value that territory more highly than a newcomer group does, such that the established group has more to gain by evicting the newcomer (and more to lose if it is evicted). Similar asymmetries have been documented in baboons (*P. cynocephalus*; Markham et al., 2012), in which the probability of winning an intergroup conflict depends partly on how frequently the group has used the area in question. Second, a group's length of tenure on the nest site may be correlated with the age and the experience of the group members. We were not able to test for this effect in our data set, but at least for stable groups (those containing the same members across years), a correlation between age of group members and tenure length on territory would be expected. Older or more experienced individuals might be more likely, or better able, to attack neighbouring groups due to differences in individual knowledge, condition or perceived value of the nesting territory. Little is known about the role that individual experience plays in group-level conflicts, although age has been shown to be a predictor of participation in intergroup contests in some primates (reviewed in Kitchen & Beehner, 2007). Finally, additional unknown variables may underlie the correlation between a group's tenure on a site and the probability of success. Groups that have nested on a territory for several years have, by definition, been able to maintain ownership of the territory and avoid eviction. It is therefore possible that long-established groups are composed of higher-quality or higher-condition individuals, and that these unknown physiological or cognitive differences are responsible for both the stability and the competitive ability of long-established groups.

In summary, the data in this study suggest that ani groups that have previously occupied a site are better able to defend that space against newcomer groups, regardless of relative group size — a pattern documented in many species of primates but (to our knowledge) never previously shown in birds. Although intergroup clutch destruction is rare, its fitness consequences are severe, always ending in the reproductive failure of the group whose clutch is destroyed. The direct fitness advantage gained by long-term occupancy of a site may therefore be significant, providing selection for group stability. Future studies are now needed to determine how long-term group membership interacts with other determinants of lifetime reproductive success, such as reproductive synchrony with fellow group members, to influence individual fitness.

Supplementary material

Supplementary material associated with this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2017.07.006.

References

Almany, G. R., De Arruda, M. P., Arthofer, W., Atallah, Z. K., Beissinger, S. R., Berumen, M. L., et al. (2009). Permanent genetic resources added to molecular ecology resources database 1 May 2009–31 July 2009. *Molecular Ecology Resources, 9*, 1460–1466.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management, 74*, 1175–1178.

Arseneau-Robar, T. J. M., Taucher, A. L., Schnider, A. B., van Schaik, C. P., & Willems, E. P. (2017). Intra- and interindividual differences in the costs and benefits of intergroup aggression in female vervet monkeys. *Animal Behaviour, 123*, 129–137.

Batchelor, T. P., & Briffa, M. (2011). Fight tactics in wood ants: Individuals in smaller groups fight harder but die faster. *Proceedings of the Royal Society B: Biological Sciences, 278*, 3243–3250.

Björklund, M., & Westman, B. (1986). Mate-guarding in the great tit: Tactics of a territorial forest-living species. *Ornis Scandinavica, 17*, 99–105.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York, NY: Springer.

Cassidy, K. A., MacNulty, D. R., Stahler, D. R., Smith, D. W., & Mech, L. D. (2015). Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. *Behavioral Ecology, 26*, 1352–1360. http://dx.doi.org/10.1093/beheco/arv081.

Cheney, D. L. (1981). Intergroup encounters among free-ranging vervet monkeys. *Folia Primatologica, 35*, 124–146. http://dx.doi.org/10.1159/000155970.

Crofoot, M. C., Gilby, I. C., Wikelski, M. C., & Kays, R. W. (2008). Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 577–581.

Emlen, S. T. (1982). The evolution of helping. I. An ecological constraints model. *American Naturalist, 119*, 29–30.

Furrer, R. D., Solomon, K., Willems, E. P., Cant, M. A., & Manser, M. B. (2011). Location and group size influence decisions in simulated intergroup encounters in banded mongooses. *Behavioral Ecology, 22*, 493–500.

Gaston, A. J. (1978). The evolution of group territorial behavior and cooperative breeding. *American Naturalist, 112*, 1091–1100.

Golabek, K. A., Ridley, A. R., & Radford, A. N. (2012). Food availability affects strength of seasonal territorial behaviour in a cooperatively breeding bird. *Animal Behaviour, 83*, 613–619.

Harris, T. R. (2010). Multiple resource values and fighting ability measures influence intergroup conflict in guerezas (*Colobus guereza*). *Animal Behaviour, 79*, 89–98.

Heinsohn, R. G. (1988). Inter-group ovicide and nest destruction in cooperatively breeding white-winged choughs. *Animal Behaviour, 36*, 1856–1857.

Jones, O. R., & Wang, J. (2010). COLONY: A program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources, 10*(3), 551–555. http://dx.doi.org/10.1111/j.1755-0998.2009.02787.x.

Kempenaers, B. (1993). The use of a breeding synchrony index. *Ornis Scandinavica, 24*, 84.

Kitchen, D. M., & Beehner, J. C. (2007). Factors affecting individual participation in group-level aggression among non-human primates. *Behaviour, 144*, 1551–1581.

Koenig, W. D., & Dickinson, J. L. (2004). *The ecology and evolution of cooperative breeding in birds*. Cambridge, U.K.: Cambridge University Press.

Lamprecht, J. (1978). The relationship between food competition and foraging group size in some larger carnivores. *Ethology, 46*, 337–343.

Lau, P., Bosque, C., & Strahl, S. D. (1998). Nest predation in relation to nest placement in the greater ani (*Crotophaga major*). *Ornitologia Neotropical, 9*, 87–92.

Lindell, C. (1996). Patterns of nest usurpation: When should species converge on nest niches? *Condor, 98*, 464–473.

Macedo, R. H. F., Cariello, M., & Muniz, L. (2001). Context and frequency of infanticide in communally breeding guira cuckoos. *Condor, 103*, 170–175.

Macedo, R. H. F., & Melo, C. (1999). Confirmation of infanticide in the communally breeding guira cuckoo. *Auk, 116*, 847–851.

Markham, A. C., Alberts, S. C., & Altmann, J. (2012). Intergroup conflict: Ecological predictors of winning and consequences of defeat in a wild primate population. *Animal Behaviour, 84*, 399–403.

Marsden, A. D., & Evans, K. L. (2004). Synchrony, asynchrony, and temporally random mating: A new method for analyzing breeding synchrony. *Behavioral Ecology, 15*, 699–700.

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo. Animal Behaviour, 78*, 359–370.

Pulliam, H. R., & Caraco, T. (1984). Living in groups: Is there an optimal group size? In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (2nd, pp. 122–147). Sunderland, MA: Sinauer.

Radford, A. N., & du Plessis, M. A. (2004). Territorial vocal rallying in the green woodhoopoe: Factors affecting contest length and outcome. *Animal Behaviour, 68*, 803–810.

Riehl, C. (2010a). Egg ejection risk and hatching asynchrony predict egg mass in a communally breeding cuckoo, the greater ani (*Crotophaga major*). *Behavioral Ecology, 21*, 676–683.

Riehl, C. (2010b). A simple rule reduces conspecific brood parasitism in a communally breeding bird. *Current Biology, 20*, 1830–1833.

Riehl, C. (2011). Living with strangers: Direct benefits favour non-kin cooperation in a communally nesting bird. *Proceedings of the Royal Society B: Biological Sciences, 278*, 1728–1735.

Riehl, C. (2012). Mating system and reproductive skew in a communally breeding cuckoo: Hard- working males do not sire more young. *Animal Behaviour, 84*, 707–714.

Riehl, C. (2016). Infanticide and within-clutch competition select for reproductive synchrony in a cooperative bird. *Evolution, 70*, 1760–1769.

Riehl, C., & Jara, L. (2009). Natural history and reproductive biology of the greater ani (*Crotophaga major*) at Gatún Lake, Panama. *Wilson Journal of Ornithology, 121*, 678–687.

Riehl, C., & Strong, M.J.. (n.d.) Stable social relationships between non-kin increase individual fitness in a cooperative bird. Manuscript in preparation.

Roth, A. M., & Cords, M. (2016). Effects of group size and contest location on the outcome and intensity of intergroup contests in wild blue monkeys. *Animal Behaviour, 113*, 49–58.

Schmaltz, G., Somers, C. M., Sharma, P., & Quinn, J. S. (2006). Non-destructive sampling of maternal DNA from the external shell of bird eggs. *Conservation Genetics, 7*, 543–549.

Seddon, N., & Tobias, J. A. (2003). Communal singing in the cooperatively breeding subdesert mesite *Monias benschi*: Evidence of numerical assessment? *Journal of Avian Biology, 34*, 72–80.

Snaith, T. V., & Chapman, C. A. (2007). Primate group size and interpreting socio-ecological models: Do folivores really play by different rules? *Evolutionary Anthropology: Issues, News, and Reviews, 16*, 94–106.

Strausberger, B. M., & Ashley, M. V. (2001). Eggs yield nuclear DNA from egg-laying female cowbirds, their embryos and offspring. *Conservation Genetics, 2*, 385–390.

Symonds, M. R., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology, 65*, 13–21.

Vehrencamp, S. L. (1977). Relative fecundity and parental effort in anis, *Crotophaga sulcirostris. Science, 197*, 403–405.

Voss, M., Shutler, D., & Werner, J. (2010). A hard look at blood sampling of birds. *Auk, 127*, 704–708.

Wilson, M. L., Kahlenberg, S. M., Wells, M., & Wrangham, R. W. (2012). Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Animal Behaviour, 83*, 277–291.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour, 75*, 262–300.

Wrangham, R. W. (1999). Evolution of coalitionary killing. *American Journal of Physical Anthropology, 42*, 1–30.