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

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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.

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).

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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 ($\leq$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

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