



## Mating system and reproductive skew in a communally breeding cuckoo: hard-working males do not sire more young

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In communally breeding animal societies, theory predicts that a male's investment in parental care should be correlated with his share of paternity in the mixed brood. Here I test this hypothesis in the greater ani, *Crotophaga major*, a Neotropical cuckoo that nests in groups composed of two to three unrelated, behaviourally monogamous pairs. Each group constructs a single nest in which all of the females lay eggs, and all group members participate in rearing the joint clutch. Previous work has shown that parental investment among males is unequal: just one male in the group performs all nocturnal incubation, and the same male also plays a greater role in diurnal incubation and nest defence. I used parentage and sibling analysis of 357 greater ani nestlings in 53 clutches to investigate genetic mating patterns and the distribution of reproduction within communal groups. Contrary to predictions, male reproductive skew was negligible and nocturnally incubating males did not sire significantly more nestlings than did non-nocturnal incubators. Approximately 75–80% of nestlings were produced by socially monogamous pairs, 12–18% by extrapair fertilizations within the same breeding group, and 3–5% by extrapair fertilizations outside the breeding group. There was no difference in the frequency of extrapair paternity between nocturnally incubating and non-nocturnally incubating males. Compared to other cooperative avian societies, the division of reproduction in greater ani breeding groups is unusually egalitarian, despite marked inequalities in male parental care.

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Communally breeding animals live in social groups in which several individuals contribute genes to a shared brood and cooperate to rear the young (Brown 1987; Vehrencamp & Quinn 2004). Group members, therefore, inevitably provide care to offspring that are not their own. In birds and mammals, these 'alloparental' behaviours typically include territory defence, incubation or baby-sitting, and lactation or food provisioning (reviewed in Stacey & Koenig 1990; Jennions & Macdonald 1994). However, the division of labour within the social group varies widely. In many societies, for example, individuals vary in the relative amounts of food that they provide to the brood (Mumme et al. 1990; Woxvold et al. 2006) or in the time spent defending the brood (Clutton-Brock et al. 1998; Gilchrist & Russell 2007). Therefore, a current question of theoretical interest is whether individual variation in alloparental care is adaptive, and whether it can be related to other fitness components such as age, reproductive output, relatedness among group members, or dominance status in the social group (Heinsohn 2004).

Understanding variation in alloparental behaviours is particularly challenging in social groups composed of unrelated individuals, in which group members cannot gain indirect fitness benefits through cooperative rearing. Because alloparental care involves substantial energetic costs, selection should favour individuals that minimize their investment in unrelated offspring (Clutton-Brock 1991; Heinsohn & Legge 1999). Therefore, traditional parental investment theory predicts that unrelated group members should adjust their levels of effort to match their share of reproduction in the mixed brood, such that individuals with higher reproductive success should also provide more care (Trivers 1972; Emlen 1978; Westneat & Sherman 1993). Early studies of some communal breeders documented striking disparities in parental effort among group members and assumed that these must necessarily reflect similar disparities in reproductive output (e.g. Brown 1970; Dow 1977; Joste et al. 1982). However, more recent studies using molecular data to quantify parentage have yielded mixed results, with some demonstrating a positive correlation between parental effort and share of parentage (Davies et al. 1992; Pöldmaa et al. 1995; Schubert et al. 2009) and others failing to detect a relationship (Jamieson et al. 1994; DeLay et al. 1996; Canestrari et al. 2005).

In this study I examine male parental care and reproductive patterns in the greater ani, *Crotophaga major*, a communally

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breeding Neotropical cuckoo. Breeding groups are composed of up to five (typically two to three) behaviourally monogamous pairs that construct a single nest in which all of the females lay their eggs. This social system provides a unique opportunity to investigate the relationship between alloparental behaviours and parentage because group members are not genetic relatives. Instead, ani groups are composed of stable coalitions of unrelated adult pairs that roost, nest and forage together during the breeding season (Bowen et al. 1989; Riehl 2011). Social nesting appears to be favoured by the antipredator benefits of communal nest defence: lone pairs are rare and never observed to be successful, and the likelihood of nest predation declines sharply with increasing group size. Groups typically defend the same nesting territory over multiple years and the majority of individuals remain with the same group (Riehl 2011).

Labour is not evenly divided among male group members. Although each breeding group typically contains either two or three adult males, just one male in each group performs all nocturnal incubation and a majority of diurnal incubation during the 12-day incubation period. Data from nest cameras and behavioural observations show that the same male (the 'nocturnal incubator') also spends a greater amount of time brooding nestlings and guarding the nest, and initiates alarm calling, communal displays and mobbing behaviours significantly more often than any other group member (Vehrencamp et al. 1986; Koford et al. 1990; Riehl & Jara 2009).

The aim of this study was to determine whether asymmetry in male parental care reflects share of paternity in the communal clutch, as suggested by the parental investment hypothesis. The genetic mating system of this species is not known and reproductive skew among male group members has not been quantified. Although male–female pairs within breeding groups appear to be socially monogamous, observations of mate guarding and attempted extrapair copulations suggest that greater anis may not be genetically monogamous. If so, variation in male reproductive success could arise through extrapair fertilizations with female group members. Males that achieve higher rates of extrapair fertilizations would, then, be expected to sire proportionately more offspring in the communal clutch and to provide higher levels of paternal care. To test this hypothesis, I used microsatellite analysis to determine genetic mating patterns and reproductive skew in a colour-banded population of greater anis over a 4-year period. My main goals were (1) to determine the genetic mating system and frequency of extrapair fertilizations within the social group; (2) to quantify levels of reproductive skew among male group members; and (3) to determine whether the nocturnally incubating male sires a higher proportion of nestlings in the communal clutch than do non-nocturnally incubating males.

## METHODS

### *Study Species and Data Collection*

The greater ani, a 150–200 g tropical cuckoo, inhabits lake, pond and river edges from central Panama to northern Argentina (Payne 2005). Nests are typically built in emergent vegetation or in low branches overhanging the water, rarely more than 2 m above the water's surface. From June to October 2006–2010, I studied a population of greater anis nesting on the shores of Lago Gatún, Panama.

Reproductive strategies and reproductive partitioning have been well studied for female greater anis, but not for males (Riehl 2010). Previous work has shown that all female group members breed and that the division of reproduction among females in the nesting group is remarkably equal. Before laying her first egg in the communal nest, each female ejects any eggs that her fellow group

members have already laid. Each female stops ejecting eggs once she has laid her first egg, so a clutch can accumulate only after all females in the group have started to lay (Vehrencamp 1977; Riehl & Jara 2009). Each female then proceeds to lay three to four eggs in the shared nest. The number of eggs per female in the final incubated clutch is, therefore, approximately equal, and reproductive 'skew' among females is extremely low (Riehl 2011).

Breeding groups of greater anis in this study area may contain up to five pairs, but groups of more than three pairs typically abandon the nest before the clutch is completed. Groups of two and three pairs are most common (ca. 61% and 32% of groups in the population, respectively; Riehl 2011). Pairs are socially monogamous and are stable within the breeding season, but pair bonds may change across years. Breeding groups typically defend the same nesting territory across multiple years. The majority of individuals remain with the same nesting group across years, but between 20% and 40% of individuals either die or switch groups from one year to the next (Riehl 2011).

All nests within the study area (between 40 and 58 nests per year) were monitored by boat from 2007 to 2009 following preliminary work in 2006. Group size was determined by counting all adults present at repeated visits to the nest. Nests were checked daily during the laying period, every 2–3 days during the incubation period, and daily during the nestling period.

Full details of colour banding, genetic sampling and nest monitoring are given in Riehl & Jara (2009). Briefly, each egg was numbered on the day that it was laid with a permanent felt-tip marker to identify its position in the communal clutch, and maternal genomic DNA was collected from blood and shed cells on the surface of the eggshell (Schmaltz et al. 2006; Riehl 2010). Each nestling was marked with a temporary, expandable plastic leg band on the day of hatching and, in most cases, matched to the egg from which it hatched. Nestlings that survived to 4–6 days of age were given a permanent combination of coloured and aluminium leg bands. A small blood sample (<100 µl) was taken by puncture of the brachial vein at 2–3 days of age, and tissue samples were taken from nestlings found dead in the nest.

Adults were trapped during the nonbreeding season (February–March), when large groups of 20–100 individuals form communal roosts on tiny (<1 ha) tree-covered islets close to the shore of the lake. Known roosting sites were surrounded by mist nets and adults were trapped at dusk as they flew in to the roost. It was possible to trap most of the individuals in breeding groups this way because adult group members tend to forage and roost together during the nonbreeding season. During the breeding season, additional mist netting was carried out near certain nests to trap unbanded group members. To obtain both nestling and adult DNA from communal groups, I directed mist-netting efforts at nests that were located in emergent vegetation and/or had been successful in a previous breeding season.

Field observations were used to identify socially monogamous pairs at nests where adult group members were colour-banded. Individuals that share pair bonds within social groups typically remain together throughout the day, foraging, perching and following one another closely. Mated pairs also allopreen and engage in courtship feeding; during nest building, each pair takes turns in constructing the communal nest. Each nest was observed at dawn or dusk at least three times to identify the nocturnally incubating male. Nests were observed for at least 1 h before sunrise until the nocturnal incubator left the nest; or for at least 1 h after sunset. At most nests (20 of 28, 71%) the identity of this male was further confirmed with motion-activated nest cameras that were placed at nests prior to the onset of incubation and remained at the nests throughout the incubation period (Wingscapes BirdCams, Alabaster, AL, U.S.A.; Riehl & Jara 2009). At all nests, the identity of

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