NATURAL HISTORY AND REPRODUCTIVE BIOLOGY OF THE COMMUNALLY BREEDING GREATER ANI (*CROTOPHAGA MAJOR*) AT GATÚN LAKE, PANAMA

CHRISTINA RIEHL[1,3] AND LAURA JARA[2]

ABSTRACT.—The Greater Ani (*Crotophaga major*) is the least well-known of the communally breeding crotophagine cuckoos, although it is locally abundant in Panama and northern South America. We present substantial new life history information from 87 breeding groups of Greater Anis at Gatún Lake, Panama, and the first description of their conspicuous, highly stereotyped communal displays. Breeding groups were composed of two to five socially monogamous pairs; no pairs nested singly. Seven groups also included an unpaired individual, which in three cases was confirmed to be a 1-year-old male from the previous year's nest. Groups of two and three pairs were most common (accounting for 75 and 20% of groups, respectively); groups containing more than three pairs were rare and their nests were abandoned before incubation began. Eggs were large (~17% of adult body mass) and varied greatly in size (19–37 g). Egg and nestling development were exceptionally rapid: eggs were incubated for 11–12 days and nestlings were capable of leaving the nest after 5 days, although adults continued to feed fledglings for several weeks. On average, each female laid 4.3 ± 0.9 eggs; three-pair groups had larger overall clutch sizes than did two-pair groups. The first 2–3 eggs to be laid were usually ejected from the nest by other group members, and number of ejected eggs increased with group size. Thirty-seven nests (43%) fledged at least one young successfully; snakes (*Pseustes*, *Spilotes*, *Boa*) and white-faced capuchin monkeys (*Cebus capuchinus*) were identified as nest predators. *Received 27 January 2009. Accepted 4 June 2009.*

The subfamily Crotophaginae (Cuculiformes: Cuculidae) consists of four species of communally breeding neotropical cuckoos (Davis 1942). Three of the four species have been subjects of long-term behavioral studies: Groove-billed Ani (*Crotophaga sulcirostris*) in Costa Rica (Vehrencamp 1977, 1978; Vehrencamp et al. 1986; Koford et al. 1990); Smooth-billed Ani (*C. ani*) in Florida and Puerto Rico (Davis 1940, Loflin 1983, Quinn and Startek-Foote 2000, Schmaltz et al. 2008); and Guira Cuckoo (*Guira guira*) in Brazil (Macedo 1992; Cariello et al. 2002, 2004; Macedo et al. 2004). Several individuals (both males and females) in all three species cooperate to build a single nest in which all of the females lay their eggs. Young generally disperse to join nearby groups rather than remaining with the natal group to breed; thus, adult breeders in groups are thought to be unrelated (Quinn et al. 1994, Vehrencamp and Quinn 2004; but see Bowen et al. 1989). Most group members participate in nest-building, territory defense, parental care, and incubation (although relative effort may differ greatly among group members), and most females appear to fledge roughly equal numbers of young.

Females in each group compete for reproduction and synchronize laying by ejecting each others' eggs from the communal nest (Vehrencamp and Quinn 2004).

Reproductive strategies within this general framework differ markedly among the three species that have been well studied. Groove-billed and Smooth-billed anis are facultatively communal: breeding groups can consist of lone pairs, multiple monogamous pairs, or multiple pairs with a variable number of non-breeding helpers (usually retained young from a previous brood; Bowen et al. 1989). The modal group size is two pairs and behavioral observations suggest that extra-pair copulations are not common within groups (Vehrencamp et al. 1986). Only early-laid eggs are ejected from the nest, probably because females are incapable of recognizing their own eggs and cease ejection once they enter the laying sequence. As a result, early-laying females lose more eggs to ejection than late-laying females (Vehrencamp 1977).

Guira Cuckoos nest in larger groups containing up to seven reproductive females; lone pairs are rare (Macedo et al. 2004). Pairs are not socially monogamous and each individual may mate with several group members, leading to genetic polygynandry. Females compete for reproduction in the nest by both egg ejection and infanticide of nestlings. Unlike anis, Guira Cuckoos eject eggs throughout the laying sequence, presumably because females are more likely to begin laying

[1] Princeton University, Department of Ecology and Evolutionary Biology, 106A Guyot Hall, Princeton, NJ 08544, USA.

[2] Universidad de los Andes, Departamento de las Ciencias Biológicas, Carrera 1A Numero 18A-10, Bogotá, Colombia.

[3] Corresponding author; e-mail: criehl@princeton.edu

asynchronously in larger, less well-organized groups. Eggs of both early and late-laying females may be ejected, and female laying order changes between clutches. The number of eggs that each female loses to competition varies from clutch to clutch, and female reproductive success tends to equalize within groups over time (Macedo 1992, Macedo et al. 2004).

Little is known about the Greater Ani (*C. major*). Conspicuous and locally abundant from eastern Panama through northern Argentina, it nests exclusively along the forested banks of lakes, rivers, and streams (Hilty and Brown 1986). Nests are built in emergent vegetation or in branches overhanging the water, and are usually accessible only by boat. Young (1925) and Davis (1941) each provided brief descriptions of one nest (from Guyana and Argentina, respectively), and noted that this species appeared to live in social groups similar to those of its congeners. More recently, Lau et al. (1998) located 27 nests along Caracol Creek, Venezuela. They found that nests built in isolated clumps of emergent vegetation were significantly less likely to be depredated than those built along the bank, presumably because the most likely predators were terrestrial rodents and wedge-capped capuchin monkeys (*Cebus olivaceus*).

Many aspects of the natural history of the Greater Ani remain unknown, including clutch size, parental behavior, egg morphology, and length of incubation and nestling periods. Basic information is also lacking on its communal breeding system, including size of nesting groups and extent of egg ejection. It is not known whether communal nesting is obligate or facultative in this species, nor whether individuals within groups form socially monogamous pairs. Our goal in this study was to provide data on these previously unrecorded life history traits through field observations of a color-banded nesting population of Greater Anis. We also wished to investigate the highly stereotyped, conspicuous social displays performed by breeding groups. This communal display has not been described in the literature aside from a brief mention by ffrench (1973).

METHODS

Study Area.—We studied Greater Anis in 2007 and 2008 at Gatún Lake, Panama, an artificial reservoir formed in 1914 when the Chagres River was dammed to create the Panama Canal. Our study area, within the 5,400-ha Barro Colorado Nature Monument, consisted of the 65-km shoreline of Barro Colorado Island and its associated smaller islands, as well as an additional ~300 km of shoreline along four adjacent mainland peninsulas (Bohio, Buena Vista, Peña Blanca, and Gigante). Barro Colorado Island and the mainland peninsulas are covered by tropical moist forest (Holdridge et al. 1971) and are deeply dissected by narrow, sheltered coves. Shoreline vegetation within these coves is dominated by *Annona glabra*, a small tree that grows in the water along the shore, and *Acrostichum danaeifolium*, a large aquatic fern (Croat 1978). Rainfall averages 275 cm annually and is strongly seasonal with a marked dry season lasting from mid-December through late April (Rand and Rand 1982). We searched for Greater Ani nests during the rainy season (May–Nov) by moving slowly along the shoreline in a small motorboat, following adults and checking emergent vegetation.

Color Banding and Group Size Assessment.— We captured adult anis at communal roost sites (during the non-breeding season) and near nests (during the breeding season) using 61-mm mesh mist nets (12 m length) on 5-m aluminum poles. Nets were mounted in shallow water parallel with the shore to capture birds as they flew across the water. We used kayaks in areas with deeper water (>1 m) to erect the nets and remove birds from nets. Nets were monitored constantly during trapping and birds were removed immediately upon capture. Each ani was banded with a unique combination of three color and one aluminum leg bands for individual recognition.

Group size was calculated by counting all adults present at each of at least three visits to the nest. All group members defend the nest and participate in communal displays in the nesting territory; group size counts were consistent and highly repeatable (estimate based on 3–8 counts at each of 85 nests: $R = 0.84$, $F_{84,170} = 182.0$, $P < 0.0001$; Lessells and Boag 1987). Groups typically consisted of socially monogamous pairs, so the number of breeding females in the group was assumed to be half the total number of individuals in the group. The ''extra'' individual was assumed to be a juvenile non-breeding helper in the few groups that consisted of an odd number of individuals (Loflin 1983, Quinn and Startek-Foote 2000, this study). The number of breeding females was assumed to be half the remaining group size

(for example, a group of 7 individuals was assumed to contain 3 breeding females). Evidence from the other *Crotophaga* spp. (Vehrencamp 1977, Loflin 1983) as well as from this species supports the assumption that all adult female group members breed. ''Group size'' refers to the number of socially monogamous pairs in the group, exclusive of helpers, unless otherwise indicated.

Nest Monitoring and Behavioral Observations.—Most nests were located prior to laying, as Greater Ani groups established territories and built nests several weeks before laying began. We checked each nest every 3–5 days until green leaves appeared in the lining, which signals the onset of laying. We then checked nests daily prior to laying and throughout the laying period. Each egg was measured with dial calipers (length and width; ± 0.1 mm), weighed on an electronic balance (± 0.1 g), and sequentially numbered with a permanent felt-tip marker to indicate position in the laying sequence. Nests were checked every 2–3 days during incubation and several times per day beginning on the expected day of hatching of the first egg. We were able to ascertain the age of nestlings to within 3–5 hrs and to match most nestlings to the eggs from which they hatched. We recorded the fate of each egg (ejected, disappeared, unhatched, hatched) and nestling (died in nest, disappeared, fledged). We opened all eggs that did not hatch and recorded them as either infertile (no embryo visible) or insufficiently developed (embryo visible). All nestlings were marked at hatching with temporary plastic leg bands, which were replaced by a permanent, unique combination of one aluminum and two color bands at 5 days of age.

We observed communal displays opportunistically during both the dry (non-breeding) and wet (breeding) seasons. We recorded locality, date, and duration of each display, as well as the number of individuals participating and the identity of color-banded birds, if present. We collected a small (<100 μl) blood sample from the brachial vein of both adults and nestlings, and stored it in lysis buffer at room temperature for molecular identification as males or females, and other genetic analyses. Genomic DNA was isolated with Qiagen DNeasy Blood and Tissue Kits (QIAGEN, Valencia, CA, USA) and all color-banded birds were identified as males or females by PCR-based amplification of an intron on the chromo-helicase-DNA (CHD) binding gene (Griffiths et al. 1998).

Nest Cameras.—We installed digital motion-activated nest cameras (Wingscapes BirdCams, Alabaster, AL, USA) at 17 nests to identify diurnal nest predators and to test pilot methods for future nest monitoring. The cameras used infrared sensors to detect motion, stored digital photographs with time and date of each photograph, and were powered by D-cell batteries. Memory cards and batteries were changed during regular nest checks; camera maintenance required <5 min/visit. We mounted cameras slightly above the nest and angled to capture images of the nest contents. We placed each camera ~1–3 m from the nest, either on an aluminum pole set in the water or, if possible, on a branch of the tree used for nesting. Cameras were generally well camouflaged by the thick vegetation surrounding the nest; it was occasionally necessary to lightly prune some vegetation to provide an unobstructed view of the nest contents. The first two cameras were placed at nests prior to laying; both nests were abandoned almost immediately. All subsequent cameras were placed at nests after clutch initiation; these nests were not abandoned. We (1) checked the images from the cameras 4 hrs after placing each camera to ensure that adults had returned to the nest and were incubating normally; (2) compared nest predation rates at the 15 nests with cameras to a randomly selected subset of 15 nests without cameras; and (3) compared nest visitation rates at three nests with cameras and at three randomly selected nests without cameras during a 5-hr period of the first morning after hatching. Visitation rates at nests without cameras were recorded by an observer with binoculars from a boat >50 m from the nest for the same 5-hr period of the first morning after hatching. Images at all 15 nests at which cameras were installed during the incubation period showed that the adults returned to the nest and resumed incubation <10 min after the camera was installed. No significant differences were found in either nest predation rates (Fisher's exact test, $P = 0.69$) or visitation rates (Mann-Whitney $U = 222$, $P = 0.67$) in comparisons between nests with and without cameras.

Data and Statistical Analyses.—We use the term ''communal clutch'' to refer to the total number of eggs or nestlings contributed by all breeding females in a nesting group, whereas ''per female clutch'' refers to the average number of eggs or nestlings contributed by an individual breeding female in a nesting group (Schmaltz et

al. 2008). It is probable that average number of eggs laid per female is not an accurate measure of individual reproductive success, as all group members may not contribute equally to a clutch. However, we present per-female averages as well as communal clutch sizes to enable comparison with previously published studies of other crotophagines (Vehrencamp 1977, 1978). Sample sizes vary because it was not possible to collect all data from every nest. Data were not normally distributed and we used non-parametric Spearman rank correlations (R_s) to examine whether communal clutch size, per female clutch size, and number of eggs ejected varied with group size. Some nests were found after laying began and survival probabilities were calculated with Mayfield's (1975) method for each stage of the nesting cycle. The nesting cycle was divided into laying period (from the day of the laying of the first egg until onset of incubation), incubation period (from onset of incubation until hatching of the first egg), nestling period (from hatching of the first egg until fledging of the first nestling), and the entire nesting period (from laying of the first egg to fledging of the last nestling). Nest predation rates for each period are presented as uncorrected percentages. Statistical analyses were performed with JMP 7.0 (SAS Institute Inc., Cary, NC, USA), all tests were two-tailed, and significance was set at $\alpha = 0.05$. Results are presented as mean ± SE unless otherwise noted.

RESULTS

Nests and Nesting Group Size.—We located and monitored 43 active nests in 2007 and 44 in 2008. An additional 28 groups defended territories and built nests, but did not lay eggs. We banded 137 adults and 221 nestlings; all individuals were color-banded in eight groups and in 14 groups at least one bird was banded. All of the 87 active nests were attended by at least two pairs: single pairs did not nest alone. Sixty-six groups (76%) consisted of two socially monogamous pairs; an unpaired adult was present at three of these. Seventeen groups (20%) consisted of three socially monogamous pairs, two of which included an unpaired adult. Three of the five unpaired helpers were 1-year-old birds that had been banded as nestlings in 2007 and were still with the natal group in 2008; molecular analyses revealed all three to be males. Only four groups (5%) included more than three pairs, and all four

nesting attempts were abandoned before incubation began.

Nesting groups formed in late April, soon after the start of the rainy season, and began building nests in early May. Close observations of four color-banded groups during the nest-building period revealed that all group members brought sticks to the nest and that nests were built quickly (between 3 and 7 days). However, most groups did not initiate egg-laying until mid-July. The earliest clutch was initiated in early June and the latest in the last week of September. Three-pair groups initiated laying later (mean date: 15 Aug, range: 10 Jul–1 Sep, $n = 17$) than did two-pair groups (mean date: 28 Jul, range: 3 Jun–18 Aug, $n = 66$). Groups frequently re-nested in the same season following depredation of the nest (up to 3 times), but groups that successfully fledged young were not observed to re-nest in the same season. Forty-four percent (19/43) of nesting territories in 2007 were re-used in 2008; group members laid eggs either in the same nest ($n = 6$) or in a different nest immediately adjacent to the old nest ($n = 13$).

All nests were built over shallow water at the shoreline. Most nests ($n = 55$) were in aquatic vegetation in the water, including *Annona glabra*, a small tree that grows in the water; *Acrostichum danaeifolium*, a large aquatic fern; and *Montrichardia arborescens*, a spiny araceous shrub. Nests were also built in a variety of deciduous trees whose branches overhung the water ($n = 32$), including *Calophyllum longifolium*, *Doliocarpus major*, *Terminalia amazonica*, *Byrsonima crassifolia*, *Coccoloba parinense*, *Clusia pratensis*, *Ficus trigonata*, and *Brosimum alicastrum*. Nests were bulky, open-cup structures of sticks lined with leaves. Adults regularly brought fresh leaves to the nest during incubation so the lining remained green, but leaves were not replaced after the chicks hatched. Measurements from a subset of five nests were: inside cup diameter mean = 16 ± 3 cm; inside cup depth mean = 7 ± 2 cm; outside cup diameter mean = 42 ± 7 cm. Nest height ranged from 0.5 to 5 m above the water's surface (mean = 1.3 ± 0.5 m).

Eggs, Ejection, and Incubation.—Eggs were elliptical to sub-elliptical in shape and turquoise-blue in color with a whitish outer layer of vaterite, a polymorph of calcium carbonate. This chalky coating was easily scratched off; freshly-laid eggs were completely white, but the coating was gradually abraded off during incubation to reveal
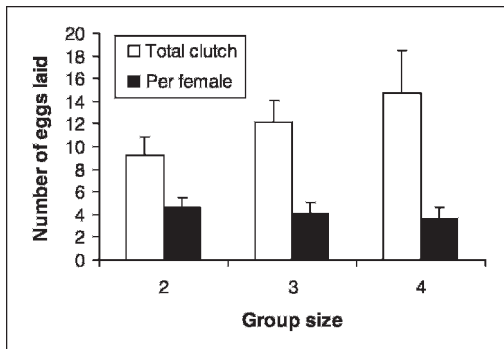
FIG. 1. Mean (+ SE) number of eggs laid (both ejected and incubated) as a function of group size in Greater Anis. Sample sizes are $n = 66$, $n = 17$, and $n = 4$ for groups of two, three, and four pairs, respectively. The number of eggs in the communal clutch significantly increased with group size, but number of eggs laid per female did not.

the bluish shell underneath. Eggs varied greatly in size, ranging from 19.3 to 37.8 g (fresh mass; mean $= 29.7 \pm 2.9$, $n = 343$). Length ranged from 38.8 to 48.1 mm (mean $= 42.9 \pm 1.7$) and width from 29.0 to 37.5 mm (mean $= 34.8 \pm 1.2$). Female body mass ranged from 155 to 201 g (mean $= 172.6 \pm 18.4$, $n = 27$); population-wide, mean egg mass represented $\sim$17% of mean female body mass. Overall, each female laid between three and seven eggs per nesting attempt (per female mean $= 4.3 \pm 0.9$) and communal clutch size ranged from 6 to 17 eggs (communal clutch mean $= 10.4 \pm 2.3$). The number of eggs in the communal clutch increased with group size (Spearman rank correlation $r_s = 0.712$, $n = 34$, $P < 0.05$; Fig. 1). However, the mean number of eggs laid per female did not vary with group size; thus, egg investment per female was roughly equal regardless of the number of females laying in the nest (Spearman rank correlation $r_s = 0.104$, $n = 34$, $P > 0.1$; Fig. 1).

The first-laid egg was ejected from the nest in all nests except one. The probability of an egg being ejected remained high throughout the laying sequence, although early-laid eggs were at greater risk (Fig. 2). On average, the first 1.7 ($\pm$ 0.9) eggs were ejected in groups with two females, and the first 4.5 ($\pm$ 1.6) eggs were ejected in groups with three females. None of the nesting attempts by groups with four or more females was successful: between 8 and 19 eggs (mean $= 14.8 \pm 3.8$) were ejected before the nest was abandoned. The number of eggs ejected per female increased with group size (Spearman rank correlation $r_s = 0.72$,
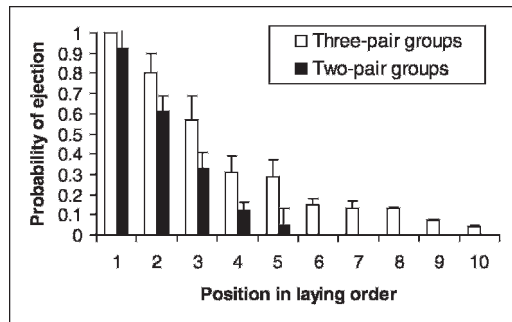

FIG. 2. Mean (+ SE) probability of egg ejection as a function of position in the laying sequence for Greater Ani nesting groups with two ($n = 66$) and three ($n = 17$) breeding pairs.

$n = 34$, $P < 0.05$; Fig. 3). Ejection typically ceased after two eggs remained in the nest for <24 hrs. Three-pair groups had higher ejection rates than two-pair groups, but ultimately incubated more eggs in the communal clutch (mean $= 9.0 \pm 1.6$ and 7.3 ± 1.1 eggs, respectively).

Each female laid an egg at $\sim$2-day intervals and females within the same group often laid eggs on alternate days. Group members typically separated into conspicuous pairs during the laying and incubation period. Incubation typically began after the third-to-last or second-to-last egg was laid, resulting in asynchronous hatching of one or more chicks ($n = 36$ clutches, 86%). Incubation began at six nests (14%) after all eggs were laid and hatching was synchronous. The time interval between hatching of the first and last egg ranged from 0 to 5 days (mean $= 2.5 \pm 0.8$ days). The
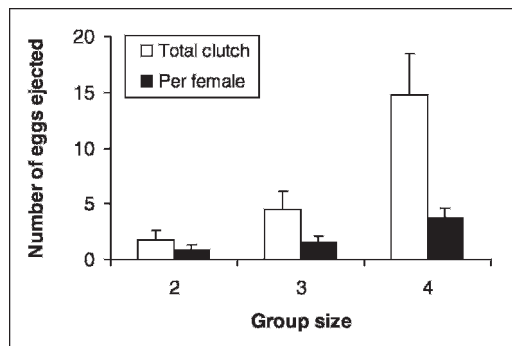

FIG. 3. Mean (+ SE) number of eggs ejected as a function of group size in Greater Anis. Sample sizes are $n = 66$, $n = 17$, and $n = 4$ for groups of two, three, and four pairs, respectively. Both group and per female losses to egg ejection significantly increased with group size.

TABLE 1. Number of eggs laid, incubated, hatched, and fledged at 24 successful Greater Ani nests at Gatún Lake, Panama (2007–2008).

	Mean ± SD	Range
Number of eggs laid	9.8 ± 2.4	6–16
Number of eggs incubated	7.8 ± 1.5	5–12
Number of eggs hatched	6.4 ± 2.3	2–10
Number of chicks fledged	4.8 ± 1.8	1–7

incubation period was 11–12 days for all 15 eggs for which we had precise information on laying and hatching times. Brood patches were present on both males and females, but we did not quantify the amount of time that each group member spent incubating.

Nestlings.—Nestlings were blind and naked at hatching; eyes opened after 1 day and pin-feathers emerged at 1–2 days. Feathers did not begin to unsheathe until 6 days, but 5-day-old nestlings were capable of climbing or jumping from the nest when disturbed. Nestlings frequently hooked their bills over twigs as they climbed, sometimes using the bend of the wing to propel themselves upwards. Nestlings often jumped from the nest into the water below, swam back to the base of the nest tree, and climbed back towards the nest. Seven-day-old nestlings readily left the nest in response to adult alarm calls. Fledging occurred at 8–10 days, when nestlings climbed from the nest into nearby vegetation. Fledglings from the same nest typically dispersed to different areas around the nest, where the adults continued to feed them for the next 2 weeks. Fledglings were capable of flying at ~14 days, when the entire group would often move to a different area away from the nest. Adults continued to feed fledglings for up to 6 weeks. Color-banded fledglings remained with their natal group for several more months before dispersing prior to the onset of the next breeding season ($n = 9$ nesting groups).

Egg and Nestling Mortality.—Overall, 43% of nests ($n = 37$) successfully fledged at least one young. Predation rates and estimated survival probabilities varied with stage in the nesting cycle (Table 1). Predation accounted for most nest losses ($n = 43$, 86%), followed by abandonment during the laying period ($n = 4$, 8%; all were groups with ≥4 egg-laying females). Two clutches (4%) failed to hatch, probably because the eggs had become wet; the eggs in both of these clutches had visible water marks on the shell where the vaterite coating had been washed away in patches.

One entire clutch (2%) was ejected from the nest during incubation for unknown reasons.

We were able to identify the predator at 9 of 43 depredated nests. At four nests we found snakes in the nest (*Pseustes poecilionotus* and *Boa constrictor*) or near the nest with a recently swallowed egg still visible in the snake's body (*P. poecilionotus* and *Spilotes pullatus*). Nest cameras confirmed snake predation at another three nests (apparently *P. poecilionotus* in all cases). We also observed white-faced capuchin monkeys (*Cebus capuchinus*) preying on ani eggs at two nests. Nest cameras were placed at an additional 18 nests that were subsequently depredated, but the cameras did not record the predator as the predation occurred at night. Nearly all nests were depredated sequentially, losing 1–2 eggs per night, and the nests were undamaged, suggesting that nocturnally active snakes were the most likely predators. On several occasions, Greater Anis also gave alarm calls when Yellow-headed Caracaras (*Milvago chimachima*) flew over, but caracara predation was not confirmed.

Egg and nestling mortality was high even in nests that successfully fledged young. We had complete information on the number of incubated eggs, number of hatched eggs, and number of fledglings at 24 nests; all of the incubated eggs hatched and survived to fledging at only two of these nests (Table 2). One or more eggs at 13 nests failed to hatch due to infertility ($n = 5$ eggs) or insufficient development ($n = 12$ eggs). Overall hatching success was 84% ($n = 196$ eggs). One or more nestlings died or disappeared before fledging at 19 nests (overall nestling survival = 76%, $n = 165$ nestlings). Four nestlings were found dead in nests, one with wounds on the body and head; a fifth was found in the nest with injuries to the head and neck, but survived. In most cases, nestlings died or disappeared in the first 2 days after hatching. Each successful nest lost an average of 1.6 chicks as a result of post-hatching mortality (± 1.4; range 0–3).

Displays.—The communal display is initiated when one individual gives a series of loud, high-pitched, cackling "kak-kaak-kak" notes, at the rate of about 3–4 syllables/sec. Other group members immediately fly in from distances as distant as 50 m to perch beside the calling individual. After several individuals have arrived, the first individual stops cackling and gives a steady, low-pitched gurgling noise similar to the

TABLE 2. Nest depredation rates and estimated survival probabilities at 87 Greater Ani nests at Gatún Lake, Panama (2007–2008).

Nesting stage	Length (days)(mean ± SE)	Estimated survival probability (%)[a]	Nest depredation (%)[b]	Number of nests[c]
Laying period	9.7 ± 3.4	58.2	23.0	87
Incubation period	11.3 ± 0.5	57.4	26.9	67
Nestling period	8.9 ± 1.4	80.2	10.2	49
Overall nest period	26.4 ± 3.9	26.8	49.4	87

[a] Computed from daily survival rates using Mayfield's (1975) method.
[b] Percentage of active nests that failed during each period because of predation.
[c] Total number of active nests monitored during each period.

sound of water boiling or the hum of an outboard motor. Other birds usually join in the gurgling call until the chorus increases in volume and intensity; during the chorus, one or more individuals may give a raspy, rising ''kaa-kaa-kaa.'' The chorus may last up to 2 min, during which time the group members arrange themselves into a loose circle on surrounding perches with their bills pointing towards the center, almost touching. Individuals in monogamous pairs typically sit next to one another with their bills closely aligned in the circle; occasionally individuals climb or hop around each other to change positions in the circle, keeping their bills towards the center. After 10 sec to 2 min, the gurgling stops abruptly and all individuals immediately disperse.

We observed 143 communal displays by 32 groups. During the non-breeding season, when Greater Anis form large communal roosts of up to 100 individuals, an average of 10.2 (± 3.1) individuals participated in each display ($n = 74$), and displays frequently involved odd numbers of birds (i.e., unpaired birds). The composition of individuals in displaying groups was not consistent; on seven occasions color-banded birds were observed to display with one group, then join a different group and later display with that group. However, displays during the breeding season involved fewer individuals and were restricted to the members of a communal nesting group (mean $= 5.2 ± 2.7$ individuals). The composition of individuals in groups was consistent during the breeding season: color-banded birds were observed to display only with their own nesting group at this time. Only socially monogamous pairs participated in displays in groups with unpaired birds during the breeding season; the unpaired bird typically sat above or near the displaying group, but did not participate. Groups usually did not display after egg-laying began, except occasionally when disturbed by observers

or by a predator at the nest. Repeated observations ($n = 22$) of displays by one group in which all members were color-banded revealed that one individual (a male) initiated ~60% of displays and that all group members participated in the displays. We usually could not attribute an obvious trigger to displays, although groups did occasionally display in response to predators at the nest or observers handling nestlings. We did not observe groups displaying in response to other groups, nor two groups displaying simultaneously.

DISCUSSION

Greater Anis, like the other crotophagine cuckoos, nest in groups composed of socially monogamous pairs that all appear to contribute eggs to a communal clutch. Female anis competed for reproduction by ejecting early-laid eggs from the nest; both clutch size and the number of eggs ejected increased with group size. Eggs were exceptionally large and variable in size, and incubation and nestling periods were extremely short. Groups with more than three breeding females were unstable, possibly due to the difficulty of synchronizing reproduction, and these nests were abandoned before a complete clutch was laid.

Greater Anis in the study population appear to be obligately communal, unlike the other crotophagine cuckoos. Greater Anis were not observed to nest as single pairs, whereas single pairs are relatively common in other *Crotophaga* (Bowen 2002, Vehrencamp and Quinn 2004). Patterns of egg investment are also different across species; the number of eggs laid per capita by Smooth-billed Anis increases significantly with group size (Schmaltz et al. 2008), whereas female Greater Anis laid roughly the same number of eggs regardless of group size.

The number of eggs that can be simultaneously incubated in one nest, as well as competition

among group members, may put an upper limit on group size. Incubated clutches contained up to 12 eggs, but no group produced more than seven fledglings—a result of fairly low hatching success combined with high nestling mortality. Partial depredation and starvation of late-hatched nestlings undoubtedly contributed to nestling mortality; however, the presence of dead and injured chicks in several nests, as well as the frequent disappearance of nestlings soon after hatching, strongly suggests that infanticide may also occur. These patterns of nestling loss are similar to those reported for the Guira Cuckoo, the only crotophagine cuckoo in which infanticide has been confirmed (Macedo and Melo 1999, Macedo et al. 2001). We were not able to confirm infanticide in this study, as cameras were not set at any of the nests in which dead chicks were subsequently found.

The conspicuous, highly stereotyped communal displays are unique to this species and warrant further research. The display itself is strikingly similar to the rallying choruses performed by cooperatively breeding Green Wood Hoopoes (*Phoeniculus purpureus*), which function as territorial contests between neighboring groups (Radford 2003). Greater Anis did not display in response to territorial encounters, however, and the function of displays may be more related to group formation, organization, and decision-making. It is significant, for example, that one male initiated a majority of displays in the one group under close observation. This male may have a role similar to that of the ''alpha'' male of the more hierarchically organized Groove-billed Ani groups, which performs a majority of incubation and nest defense (Vehrencamp 1977). More observations of color-banded individuals and nesting groups are needed to clarify the role of this behavior.

The data presented here represent preliminary results from an ongoing study of the genetic mating system of Greater Anis. Future work on this color-banded population will attempt to quantify reproductive success of individuals within groups by combining field observations with genetic data to identify paternity and maternity of nestlings.

ACKNOWLEDGMENTS

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