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Competition and waste in the communally breeding smooth-billed ani: effects of group size on egg-laying behaviour

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We investigated the effects of group size on egg-laying behaviour in the communally breeding, joint-nesting smooth-billed ani, *Crotophaga ani*. We tested the predictions of the competitive female egg-investment hypothesis, which states that females in plurally breeding, joint-nesting systems respond to increased group size and egg-laying competition by trying to skew the contents of the final incubated clutch of eggs in their own favour by tossing and/or burying competitors' eggs and by producing more of their own eggs. Results supported the predictions of the hypothesis as both the number of eggs produced per capita and the number of eggs lost per capita increased with increasing group size. Egg tossing and burial behaviours were almost entirely restricted to multifemale groups and 56% of the 829 eggs laid in communal nests were lost to either egg tossing or burial. As a consequence of this egg-laying competition, the number of eggs incubated per capita decreased with increasing group size. Large groups laid more eggs and took more time to synchronize laying than smaller groups. Finally, we found that chicks hatched late within a communal clutch were more likely than earlier hatching chicks to die during the first 5 days of life. We conclude that communal life in anis generates competition and egg production waste that reduces short-term per capita reproductive benefits. Long-term data are needed to clarify individual benefits associated with communal breeding in this species.

Keywords: asynchrony; communal breeding; competition; *Crotophaga ani*; group living; laying synchrony; offspring mortality; smooth-billed ani

The determinants of clutch size in animals have fascinated ecologists for over six decades and the theory of optimal clutch size has generated much interest and research in behavioural ecology since its inception. Lack (1947, 1954) proposed that clutch size should reflect the maximum number of young that adults can raise. In certain communally breeding mammals, communal rearing allows mothers to invest in pups at a reduced cost since rearing is shared (Hayes & Solomon 2004). In birds, most questions related to optimal clutch size theory have centred on productivity of a single clutch of eggs, but some have looked at the influence of clutch size on lifetime reproductive success (Monaghan & Nager 1997). Clutch or litter size has been found to vary with environmental factors such as food availability (Hussell & Quinney 1987; Bolton et al. 1993; Hayes & Solomon 2004), latitude (Young 1994; Fargallo & Johnston 1997), seasonality (Lack 1954; Crick et al. 1993), predation (Lima 1987) and female quality (age: Afton 1984; body condition: Bolton et al. 1993; breeding experience: Klomp 1970). Most studies of avian clutch size to date have focused on species in which females nest singly or with their mate. In communal joint-nesting species, two or more females lay eggs and rear young in the same nest (Brown 1987; Vehrencamp & Quinn 2004). In most communal joint-nesters, and certain communally breeding mammals, life in groups creates competition among adults (Koford et al. 1990; Macedo 1992; Koenig et al. 1995; Gilchrist 2006). Since more eggs are laid than can be successfully incubated to produce hatchlings, adults compete over which eggs will be incubated (Vehrencamp & Quinn 2004). In such

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groups, females benefit by adjusting clutch size and egg-laying behaviour to maximize their own fitness. In guira cuckoos, *Guira guira*, where up to seven females share a nest, competition is manifested through egg tossing and nestling infanticide (Macedo & Melo 1999; Cariello et al. 2002). Eggs laid early during the nesting effort are typically tossed, but egg loss also occurs throughout egg laying and incubation (Macedo 1992; Macedo et al. 2004a). Such egg losses and infanticide can occur when females breed alone, although the probability is low (Macedo 1992; Macedo et al. 2004a).

Smooth-billed anis, *Crotophaga ani*, are communal joint-nesters that are socially monogamous (Quinn & Startek-Foote 2000). Ani group sizes can range from two to 17 adults with up to five females laying eggs in the same nest (Quinn & Startek-Foote 2000). Group size is known to average 6.7 individuals in Florida, U.S.A. (Loflin 1983) and females can lay from three to seven eggs with an average of five eggs per female (Loflin 1983). Adult group members are generally not related to each other and cooperate in defending the territory and rearing young (Quinn & Startek-Foote 2000). As in guira cuckoos, acorn woodpeckers, *Melanerpes formicivorus*, and groove-billed anis, *Crotophaga sulcirostris*, smooth-billed anis compete for access to the incubated clutch of eggs by tossing eggs out of the nest (Loflin 1983; Quinn & Startek-Foote 2000; Haydock & Koenig 2002; Macedo et al. 2004a; Vehrencamp & Quinn 2004). However, smooth-billed anis also compete by burying many eggs into the nest structure (Quinn & Startek-Foote 2000). In a study of 41 communal nests in Florida, 37% of eggs laid were tossed, while 38% of eggs laid were buried (Loflin 1983). In groove-billed anis, communal joint-nesting females are thought to perform most of the egg tossing/burial (Vehrencamp 1977), although the contribution of each sex has yet to be quantified. Apparently, in groove-billed anis and guira cuckoos, individual females stop destroying eggs when they start laying, possibly to avoid mistakenly destroying their own because they do not seem to recognize their own eggs (Vehrencamp 1977; Cariello et al. 2004).

In this study, we examined influences of group size on egg-laying behaviour and competition in smooth-billed anis. The main objective of our study was to determine whether the number of laying females (i.e. female group size) significantly affects nesting variables such as breeding synchrony, number of eggs laid and egg loss probabilities within the laying sequence. Given such effects, we examined how individuals adjust their egg-laying behaviour in response to the heightened competition and conflict.

We propose a new hypothesis, the competitive female egg-investment hypothesis, to try to explain the effect of group size on egg-laying behaviour. This hypothesis states that females in multifemale groups respond to increased group size and competition by trying to skew the contents of the final incubated clutch of eggs in their favour by tossing and/or burying competitors' eggs while producing more of their own eggs. This hypothesis predicts different female strategies in single versus multifemale groups.

(1) The number of eggs produced per capita should increase with the number of females per group (female group size).

(2) The number of eggs lost to tossing and burial per capita should increase with female group size.

(3) Egg tossing and burial should be restricted to multifemale groups.

METHODS

Study Sites

We studied smooth-billed anis at the Cabo Rojo and Laguna Cartagena National Wildlife refuges in southwestern Puerto Rico (17°59′N, 67°10′W, elevation 2–42 m, 18°01′N, 67°06′W, elevation 55–71 m) from 2000 to 2004 during the rainy season when most ani breeding occurs (September–January). The southwestern portion of Puerto Rico has a dry tropical climate, and both Cabo Rojo (587 acres) and Laguna Cartagena (794 acres) refuges contain second-growth dry scrubland, and open and disturbed habitats that attract breeding anis (Loflin 1983; Quinn & Startek-Foote 2000). During the 5-year study, we followed the fate of 41 nests at Cabo Rojo and 18 nests at Laguna Cartagena. Those 59 nest-years represent a total of 38 different breeding locations. The majority of nests under study were found in 2003 and 2004 (21 and 18 nests, respectively). These two field sites are ideally suited to test the predictions of the female egg-investment hypothesis since both single and joint-nesting females breed within the same population at these two locations.

Banding and Group Size Determination

Adults were captured using either two 1.9 cm mesh mist nets (18 m length) set one directly above the other on 7.2 m high telescoping poles (Meyers & Pardieck 1993), a nest trap (Mock et al. 1999), or a hardware cloth funnel trap containing a caged hand-reared lure bird placed within a group's territory before or during nesting (Vehrencamp 1977). After capture, birds were blood sampled, measured and banded with a unique combination of one numbered metal and three colour bands. For the 59 groups under study, adult group size was counted before, during and after nesting effort, recording both total number of birds and number of banded and unbanded adults whenever visible during each visit to the group's territory (typically every other day). For ani groups where all group members were caught ($N = 16$), female group size was determined by the analysis of blood samples that were sexed by amplifying an intron in the Chromo-Helicase-DNA (CHD) binding gene (Griffiths et al. 1998). For the other groups ($N = 43$), female group size was calculated by dividing adult group size by two since anis show pairing behaviour and are socially monogamous within groups (Quinn & Startek-Foote 2000). In case of odd group sizes, female group size was assigned to the lower round number (i.e. group size of 11 birds contained an estimate of 5 females). This approach matched the data for fully sampled groups ($N = 16$) with a slight male bias 1.19:1 (M:F) also found elsewhere for anis (Davis 1940; Skutch 1959). Four groups under study had two nests with a full clutch within a breeding season. Since group composition