NESTLING PROVISIONING IN SMOOTH-BILLED ANIS

NESTLING PROVISIONING IN A JOINT NESTING CUCKOO: THE SMOOTH-BILLED ANI (*CROTOPHAGA ANI*)

By

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iii

Table of Contents

List of Tables	v
List of Figures	vi
Chapter I	1
References	4
Chapter II	5
Abstract	5
Introduction	6
Methods	10
Results	17
Discussion	18
Acknowledgements	22
Tables and Figures	23
References	31
Chapter III	36
Overview of offspring recognition and discrimination	36
Offspring recognition and discrimination in a joint nesting cuckoo	40
Video-monitoring protocol	44
References	47

List of Tables

Table 1. Summary of multiple regression models of nestling provisioning frequency and periodicity.

Table 2. Adult group sizes and parameters of the maximum time interval (max interval) and the average of five maximum time intervals (avg max interval) between feedings (mean, standard deviation and coefficients of variance [coeff of variance]) for ten video monitored groups.

List of Figures

Figure 1. Bi-variate plot of delivery rates (items of food per hour) for the first three hours after nocturnal incubation versus delivery rates for the remaining (approximately seven) hours of daylight ($r^2 = 89.9\%$, F = 63.53, P < 0.001).

Figure 2. Bi-variate plot of total delivery rate (items of food per hour) as a function of brood size (multiple regression model: F = 14.22, $r^2 = 81.1\%$, P < 0.001, adult group size: T = -0.21, P = 0.835, brood size: T = 9.38, P < 0.001).

Figure 3. Bi-variate plot of per capita delivery rate (items of food per hour) as a function of brood size (multiple regression model: F = 12.92, $r^2 = 79.5\%$, P < 0.001, adult group size: T = -4.27, P < 0.001, brood size: T = 6.23, P < 0.001).

Figure 4. Bi-variate plot of total delivery rate (items of food per hour) as a function of adult group size (multiple regression model: F = 14.22, $r^2 = 81.1\%$, P < 0.001, adult group size: T = -0.21, P = 0.835, brood size: T = 9.38, P < 0.001).

Figure 5. Bi-variate plot of per capita delivery rate (items of food per hour) as a function of adult group size (multiple regression model: F = 12.92, $r^2 = 79.5\%$, P < 0.001, adult group size: T = -4.27, P < 0.001, brood size: T = 6.23, P < 0.001).

Figure 6. Boxplot of time intervals (minutes) between consecutive feedings for nestling provisioning observations at ten video monitored nests, arranged randomly. Median (horizontal bar), interquartile range (shaded inner box) and range (outer box) shown.

Chapter I:

Smooth-billed anis (Crotophaga ani)

The smooth-billed ani (*Crotophaga ani*) is a cuckoo of the sub-family Crotophaginae, a group that also includes groove-billed anis (*C. sulcirostris*), greater anis (*C. major*) and guira cuckoos (*Guira guira*). Unlike other cuckoos, members of Crotophaginae are neither simple monogamous breeders, nor brood parasites; they are communal. Social groups consist of multiple breeding pairs that share a single nest. Social breeding groups numbering from three to 17 mostly unrelated co-breeders defend a territory during the breeding season, which is from September to January in Puerto Rico (Quinn and Startek-Foote 2000, Vehrencamp and Quinn 2004). Some individuals return to the same territory year after year, whereas others disperse (Quinn unpublished data). Occasionally, young that fail to disperse remain on their natal territory (Quinn unpublished data).

Smooth-billed anis are joint nesters, which means that more than one female lays eggs in the group's shared nest. They have biparental care; however, a single male assumes all nocturnal incubation with few exceptions (Quinn and Startek-Foote 2000, Vehrencamp and Quinn 2004). Adults form social pairs, but are not genetically monogamous, as females have extra-pair young with other males from their breeding group (Blanchard 2000). Communal breeding groups of smooth-billed anis have medium to low reproductive skew and it does not appear that dominants of either sex control reproduction (Vehrencamp 2000, Magrath *et al.* 2004). In contrast, cooperative breeding groups, like helper-at-the-nest systems, have high reproductive skew, which means only

MSc Thesis – A Samuelsen

McMaster - Biology

one breeding pair breeds whereas other group members simply help provide parental care (Magrath *et al.* 2004, Vehrencamp and Quinn 2004).

Smooth-billed anis are resident breeders of southern Florida, the Caribbean, Central America and South America (Quinn and Startek-Foote 2000). Although they can breed year-round, their main breeding season coincides with the abundance of prey that occurs after the rainy season (September to January in Puerto Rico). Prey items include insects (grasshoppers, katydids, butterflies, moths and caterpillars), garden spiders (*Argiope* spp.) and anoles (*Anolis* spp., Davis 1940). Anis build open cup nests of branches and twigs, which are lined with fresh green leaves. Trees with thorns are preferred for nesting (*e.g.* mesquite [*Prosopis pallida*] and rólon [*Pithecellobium dulce*]), and nest height varies from 2 to > 10 m off the ground (Quinn and Startek-Foote 2000). Freshly laid ani eggs are solid white, but the white calcite that coats the blue egg scratches off as eggs are moved around the nest (Davis 1940).

Egg tossing and burial are products of female competition in crotophagine cuckoo breeding groups with more than one female (Schmaltz *et al.* 2008, Vehrencamp 1977), although observations indicate that males toss eggs as well (Quinn unpublished data). Females that lay their eggs earliest in the incubated clutch are more likely to have their nestlings hatch first, and may have an advantage over late-laying females if their eggs are not destroyed because their nestlings may be larger and more successful at competing for food. Schmaltz *et al.* (2008) found that nestlings that were among the first to hatch were more likely to survive to five days than late-hatching nestlings. However, eggs laid early were also more likely to be buried or tossed by other group members. Vehrencamp

MSc Thesis – A Samuelsen McMaster – Biology

(1977) reported all early-laid eggs being tossed within two days of laying in groovebilled anis. It is likely that females that have not begun laying eggs attempt to toss or bury other female's eggs until they themselves are ready to lay. Egg tossing and burial usually end when females have synchronized their laying, a task that usually takes longer in large groups (Schmaltz *et al.* 2008). In smooth- and groove-billed anis, the number of eggs that are laid and that are lost per female are both higher in larger groups. In smoothbilled anis, the number of surviving incubated eggs per female decreases in larger groups (Schmaltz *et al.* 2008); however, the number of surviving incubated eggs per female remains the same across all adult group sizes in groove-billed anis (Vehrencamp 1977).

Joint nesting breeding groups of smooth-billed anis present a novel situation within which to study parental care, specifically nestling provisioning. Group dynamics are unlike most other cooperative systems because breeding groups consist of mostly unrelated co-breeders rather than kin. In this thesis I explore the effects of adult group size on two aspects of nestling provisioning, and also discuss potential research on nestling discrimination.

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Chapter II:

Group size effects on nestling provisioning in a joint nesting cooperative breeder: the smooth-billed ani (*Crotophaga ani*)

Abstract

Joint nesting is a form of cooperative breeding in which multiple females of a group of co-breeders contribute eggs, all laid in a single shared nest that is cared for by the group. Costs associated with this type of group living include egg tossing and burial; however, benefits have not been thoroughly explored. Group living may afford adults the ability to either increase total care delivered to young or reduce their individual share of parental care. Either strategy may be a factor in explaining joint nesting. We observed fifteen groups of smooth-billed anis (Crotophaga ani), a joint nesting cuckoo, that varied in size from two to 11 adults. Ten were monitored with video cameras and five were observed directly. We tested the effect that adult group size had on the frequency and periodicity of nestling provisioning. We explored the effect of adult group size on both total and per capita food delivery rates at these 15 nests. Total food delivery was related to brood size, but not adult group size, and total food delivery per capita was related to both brood and adult group size. Therefore, adults in larger groups provisioned less frequently than those in smaller groups, an effect referred to as load lightening. Nestling growth rates were independent of adult group size. We also used data collected from our ten video monitored nests to examine variation in waiting time between feeding events (i.e. feeding periodicity) as related to adult group size. The time intervals between food deliveries

were variable, but neither the coefficient of variation or the average maximum time interval were related to adult group size, suggesting that other factors may be more important in determining the intervals at which nestlings are fed for this species. The relationship between food delivery rate per capita and adult group size is analogous to the load lightening or compensatory response described for helper-at-the-nest systems. To our knowledge, our findings are the first to demonstrate this effect in a joint nesting species.

Introduction

Parents respond to the provisioning needs of their brood, but in cooperatively breeding species, also appear to be sensitive to the contributions of additional group members (Komdeur 1994, Hatchwell 1999). In helper-at-the-nest systems, breeding pairs generally adopt one of two strategies when assisted by helpers (reviewed in Hatchwell 1999, but see Valencia *et al.* 2006): they either reduce their individual provisioning work load in accordance with the number of helpers that assist with provisioning, which means nestlings receive the same amount of food regardless of adult group size (*i.e.* load lightening or compensatory effect), or they maintain their individual provisioning rates regardless of the number of helpers, which means nestlings receive more food as adult group size increases (*i.e.* additive effect, Hatchwell 1999). Adults usually reduce their individual provisioning rates when helpers assist with food delivery when the main threat to brood survival is nestling depredation. This effectively maintains the number of nest visits, which may avoid increased attraction of nest predators as more individuals join the

group. In contrast, adults in groups tend to maintain their individual provisioning rates when success is limited by nestling starvation. This increases food delivery and may reduce nestling starvation (Hatchwell 1999). The red-throated bee eater (*Merops bullocki*) is a cooperative bird that has been found to adopt both of these strategies depending on the breeding conditions. Under poor breeding conditions (*e.g.* adverse weather), parents maintained their nestling provisioning rates when helpers were present, which improved survival for broods with helpers (Dyer 1979 as cited by Crick 1992). Under good breeding conditions, parents decreased their provisioning work load, and there was no difference in survival of broods with or without helpers (Crick and Fry 1986).

Many cooperative birds form groups that consist of one breeding pair and at least one helper (often kin) that assists with parental care but does not breed (Cockburn 1998). However, there are other cooperative birds that form groups that consist of mostly unrelated individuals, all or most of which co-breed in a single nest and work together to provide care for their communal brood (Vehrencamp 2000, Vehrencamp and Quinn 2004). This type of breeding, referred to as plural joint nesting or communal nesting (hereafter joint nesting), has been observed in few avian taxa, namely cuckoos of the subfamily Crotophaginae, acorn woodpeckers (*Melanerpes formicivorus*, Mumme *et al.* 1988), pukekos (*Porphyrio porphyrio*, Jamieson *et al.* 1994), and Taiwan yuhinas (*Yuhina brunneiceps*, Yuan *et al.* 2005). While the effects that helpers have on nestling provisioning in avian helper-at-the-nest systems have received considerable attention, the effects of co-breeders in joint nesting systems have received little, if any.

Joint nesting appears costly, especially for females, because many of the eggs that are laid are lost to egg tossing and burial. Egg tossing and burial occur in groups with two or more females, which suggests that females compete with each other, possibly to skew nest contents in their favour (smooth-billed anis Schmaltz *et al.* 2008, groove-billed anis Vehrencamp 1977, guira cuckoos Quinn *et al.* 1994 and acorn woodpeckers Koenig *et al.* 1995). One study reports a loss of 56% of eggs to either tossing or burial in smooth-billed anis (Schmaltz *et al.* 2008). Anis that breed as lone pairs are not subject to this loss, and egg tossing and burial are less intensive in smaller groups.

Benefits that may offset costs associated with female competition in joint nesters are not fully understood. Groups of joint nesting smooth-billed anis consist mostly of unrelated co-breeders; therefore, any benefits gained through group living are not likely achieved through indirect fitness, as they are in helper-at-the-nest systems. However, it is possible that joint nesters allow themselves to reduce their individual parental effort when they nest with large groups, in a way similar to the compensatory or load lightening strategy that has been reported in helper-at-the-nest species. Large joint nesting groups may realize reduced costs associated with reproductive tasks such as nest building, incubating and especially nestling provisioning because the work load can be shared among group members. Adults that work less at provisioning can use their time for other activities, such as defending the nest or territory against predators or intruders and foraging. These activities may in turn increase longevity (Brown 1978, Crick 1992). Alternatively, adults in large groups may benefit if their young receive additional parental

care from additional group members. Nestlings that receive more care at the nest may be more likely to survive and recruit into the breeding population (Magrath 1991).

Another aspect of nestling provisioning is provisioning periodicity. Sometimes referred to as provisioning constancy, periodicity is the regularity or variability of the time intervals between consecutive feedings. Long time gaps between feedings may be physiologically stressful and are potentially deadly for nestlings that do not have adequate nutritional or fat reserves. In many pelagic seabirds, nestling survival is related to how long nestlings have to wait between food deliveries; nestlings with inadequate fat stores that wait long periods for food are less likely to survive (Hamer and Thompson 2008). Studies on nestling provisioning periodicity have focused on seabirds, and no studies have looked at the effect of adult group size on periodicity. Adult group size may be indirectly related to provisioning periodicity as vigilance may be improved in larger groups, which may allow adults to forage more efficiently, and bring food to the nest at more regular time intervals. Consequently, there should be fewer long time-gaps between food deliveries in larger groups.

In this study we explored the effect of adult group size on nestling provisioning in a joint nesting cuckoo, the smooth-billed ani, to test hypotheses related to provisioning in communal groups. We explored the relationship between adult group size and both the frequency and the periodicity of food deliveries. If adults responded to group living with a compensatory or load-lightening effect we expected that total food deliveries would not increase as a function of adult group size, that the number of food deliveries per capita would decrease with adult group size, and that nestling growth rates would be

independent of adult group size after controlling for brood size and nestling age. If the response was additive, we expected larger groups to have more total deliveries than small groups, and as a result, we expected nestlings in large groups to grow faster. We also expected to see less variation in the measures of time intervals between nestling feedings in larger groups than in smaller groups.

Methods

Study site

Smooth-billed ani populations at our primary and secondary field sites in south-western Puerto Rico, Cabo Rojo and Laguna Cartegena National Wildlife Refuges (NWR), respectively, have been monitored during their peak breeding season (September to January) on a yearly basis since 1998. Cabo Rojo NWR is tropical dry forest mixed with grassland and is bordered by privately owned and pastureland. Laguna Cartegena NWR, which rests at the base of the Sierra Bermejas mountain range, has tropical forest mixed with grassland and is located near a fresh water lagoon. For detailed descriptions of both field sites see Schmaltz *et al.* (2008). Each year since 1998, we have monitored up to 25 breeding groups on Cabo Rojo NWR. See Quinn and Startek-Foote (2000) for a detailed description of the study species.

Adult capture and group-monitoring

Breeding groups were identified at the beginning of and monitored throughout each breeding season. All groups at Cabo Rojo NWR were censused approximately once a

month to determine adult group size and to identify banded individuals. Groups at Laguna Cartegena NWR were also monitored, but only if their nests were selected for video monitoring. Three different methods were used to capture adults. Anis respond aggressively to intruders in their territories making it possible to lure them into a cylindrical hardware cloth funnel trap using a hand raised conspecific as a lure bird (McClure 1984). We also used stacked mist nets (two nets mesh size 60 mm, length 18 m set one above the other) set up on telescoping poles to intercept adults entering or exiting night roosts. When possible we used a nest trap to capture adults as well (Mock et al. 1999). Adults were banded with a unique combination of three plastic colour bands and a plain or anodized (i.e. coloured) aluminum band. Bills were marked (on both sides starting in 2007) with white non-toxic acrylic nail polish to facilitate identification in the field and on video tapes. When possible, a radio transmitter (weighing < 2 g, *i.e.* < 3%body weight; Holohil Systems, Ltd., Carp, Ontario) was attached to one adult within a group with a figure-eight harness using three to six strands of embroidery thread (Rappole and Tipton 1990) to facilitate group monitoring and nest searching.

Nestling provisioning

Smooth-billed ani nests are built from branches and twigs, and are lined with green leaves. Trees with thorns (*e.g.* mesquite [*Prosopis pallida*] and rólon [*Pithecellobium dulce*]) are preferred for nesting; nest height varies from two to greater than ten metres (Quinn and Startek-Foote 2000). Nests were located by visual searches and by observing adult behaviours that were directed in the area of the nest. Nests were checked

approximately every second day. Visits were made daily near the expected hatch date to determine the hatch date of the first nestling. Nestlings were measured (see below), weighed and marked at every nest check. Each nestling in a brood was given a different mark with non-toxic acrylic nail polish for individual recognition on subsequent nest visits and on video recordings. Acrylic markings were re-applied on each subsequent visit, as the marks tended to crack and fall off the skin quickly.

Starting in 2002, some nests that were selected based on nest suitability for camera setups were video monitored with small colour/infra-red time lapse video cameras (Sandpiper Designs, Inc., Manteca, California), and in 2007 five nests that were selected based on availability of observers and viewability of the nests were observed directly. From 22 video monitored nests, ten met the following criteria for this study: 1) known adult group size, 2) known hatch date for first nestling, and 3) nestlings present and visible. Nests were from five different years: 2002 (1), 2003 (3), 2004 (3), 2005 (1), and 2007 (2). One nest was located at Laguna Cartegena NWR ("Bimbo" 2003); all others were from Cabo Rojo NWR. Cameras were set up at least 30 cm from the nest cup; nest abandonment never coincided with camera setup. Each nest was observed for a maximum of 180 minutes per day starting when the nocturnal incubator stopped brooding (between 5:40 and 7:50). We selected this interval because of time restrictions in both the field for direct observations and in the lab for video reviewing. We chose the first three hours of the day, rather than another time period because we assumed all nestlings would be hungry, and their and the adults' behaviours would not be altered by what had happened earlier in the day. Moreover, nestling provisioning was more intensive during

the morning, as opposed to other parts of the day. Using a sub-sample of eight days of sample nest video monitoring periods that were selected randomly, we found that the three hour period reflected provisioning frequency for the remaining hours in the day. We found a tight relationship between feeding frequency of the first three hours and that of the last seven hours (Regression: $r^2 = 89.9\%$, F = 63.53, P < 0.001, Fig 1). Nests were monitored for a total of 432.7 ± 231.6 minutes (range 173 to 835 minutes) over a maximum period of five consecutive days, with the oldest nestling being no more than six days old. All video cassettes were reviewed by the same individual (AS) to determine the number of visits adults made to the nest, the number of times adults brought food to the nest, and the number of times nestlings were fed. Prey items were identified and sized relative to adult beak size following guidelines found in Schwagmeyer and Mock (2008). Prey items were categorized as either small, medium or large; small prey were approximately 0.75 cm or less in length, medium prey were between approximately 0.75 and 2 cm, and large prey were greater than 2 cm. For six groups we were able to determine the identity of adults bringing food to the nest for every visit, so it was possible to determine the relative contribution of each adult in a group. All adults contributed approximately the same amount for all but one nest ("4-way" 2005), in which three young from the previous year that had not dispersed from their natal territory did not provision as frequently as adults; exclusion of said nest from our analysis had no significant effect on our results.

Provisioning data were also collected for five nests that were observed directly by AS and two field assistants in 2007. Observers sat close enough to have a clear view of

adults coming to the nest without disturbing the group (as close as 10 m in dense vegetation, and as far as 100 m across an open field) and counted the number of visits adults made to the nest for three hours starting once the nocturnal incubator first left the nest in the morning. Video observations revealed that food was not brought at every nest visit, and that food items were sometimes refused by nestlings and eaten by the provisioner. To allow comparison of video data and direct observations we adjusted data collected from direct observations based on a regression of the number of nest visits against the number of times nestlings were fed according to video observations (n = 10 nests, $r^2 = 90.0\%$, F = 71.98, P < 0.001).

Independent variables for analyses of provisioning rates were defined as follows: 1) adult group size: the number of adults roosting in the same roost at night, as determined by monthly censusing, plus the nocturnal incubator (if incubating or brooding), and 2) brood size: the number of nestlings present in the nest as seen in videos or determined from nest checks. Two territories were monitored in more than one year, in which one or more group member was the same for each nesting attempt ("4-way" observed in three different years and "Home" observed in two different years). Moreover, multiple entries per nest were included for different days within the same year and for different brood sizes on the same day (as nestlings hatched). To control for repeated measurements of delivery rate at the same nest we included territory as a dummy variable in our analyses (Hardy 1993). Year, hatch date and the number of days since the first nestling hatched were originally considered as independent variables, but were excluded from the final analysis because they did not explain significant variance in

the models. The number of days since the first nestling hatched, intended as a measure of brood age, may have been non-significant because it over-estimated actual differences in average brood age. Brood size changed over daily observation periods as eggs hatched. Because we specified brood size it was necessary to consider an observation period during which the groups brood size remained constant as the sample unit. For provisioning frequency, our dependent variable was delivery rate, which was either expressed as the total number of food deliveries to a nest per hour, or the number of food deliveries made per hour per capita (based on number of adults in the group). We tested the effect adult group size had on provisioning periodicity using two different dependent variables: 1) the coefficient of variation for nestling provisioning at each nest, which was calculated by dividing the mean time interval between feedings by the standard deviation, and 2) the average of the five maximum time intervals between consecutive food deliveries considering all observations of a nest.

Our fifteen focal nests varied in adult group size (average 5.5, range 2-11 cobreeders) and brood size (average 4.9, range 1-9 nestlings).

Nestling growth rates

To determine hatching date of the first nestling, it was necessary to visit nests daily starting a few days before the expected hatch date. Subsequent nest visits took place every one to five days (mode two days) until nestlings fledged. Measurements were not taken at the same time each day, and were not always taken at regular intervals. Because our study nests were checked irregularly, some nestlings were measured up to seven

times, while others were only measured twice between hatch date and the last day nests were visited (day nine). Four morphological measurements were taken at every nest check (mass, head to tip of the upper bill length, exposed culmen length, and tarsus length); however, only two, mass and exposed culmen length, were used to calculate growth rates, as head-to-tip and tarsus length measurements varied between field personnel.

Growth rates were linear during the nestling period (days 0-9, personal observation; therefore, we were able to calculate growth rates as the slope of a linear regression relating mass or exposed culmen length to nestling age. Smooth-billed ani nestlings hatch asynchronously, with up to five days between the first- and last-hatched for nests reported here, but growth rates did not differ between hatching ranks. Growth rates were measured as the change in mass or length divided by the number of days between the first and last measurement. We calculated average nestling growth rates for each brood for the 15 nests for which we had provisioning data, as well as for eight additional nests for which we had mass and exposed culmen length measurements. We used nestling growth rates in two analyses. The first was to test the relationship between adult group size and growth rates, and the second was to test the relationship between nestling provisioning frequency and growth rates.

Statistical analysis

We used JMP 7 (SAS Institute Inc., Cary, North Carolina) for statistical analysis. Means are presented with standard deviations. For provisioning frequency, we used a stepwise

regression using both forward and backward elimination of non-significant variables to simplify our model. Brood size was included in all multiple regressions to control for the number of nestlings because it had a significant effect on both provisioning frequency and periodicity. All r^2 values are adjusted values, which account for the number of predictors in the model (SAS 7).

Our provisioning periodicity data were highly skewed and could not be normalized with transformations; therefore, non-parametric statistics were used to determine if periodicity of nestling provisioning differed among nests.

Results

Brood size was a significant predictor in most provisioning models, which are summarized in Table 1. Both measures of nestling provisioning frequency increased with brood size (Figs 2 and 3), whereas provisioning periodicity decreased with brood size (*i.e.* time intervals were more variable in large broods). Total delivery rate was not significantly related to adult group size; however, there was a significant negative relationship between delivery rate per capita and adult group size (Table 1, Figs 4 and 5).

Time intervals between food deliveries ranged from 0 to 151 minutes, whereas coefficients of variation ranged from 0.7 to 1.2 (Table 2). The range of time intervals between consecutive food deliveries differed significantly among nests (Kruskal-Wallis, H = 60.79, P < 0.001, Fig 6), but this difference was not explained by adult group size when we controlled for brood size (Table 1). The relationships between the maximum

time interval or the average of five maximum intervals and adult group size were also not significant (Table 1).

Nestlings were measured over a maximum period of nine days (the maximum number of days they spent in the nest) to determine growth rates. Nestling culmens increased on average 1.1 ± 0.2 mm/day in length (n = 23 broods, range 0.7 to 1.7 mm) and nestlings gained 4.7 ± 1.5 g/day (n = 30 broods, range 0 – 7.6 g). Nestling growth rates were not related to adult group size (culmen: n = 21, Pearson's r = -0.328, *P* = 0.147; mass: n = 20, Pearson's r = 0.146, *P* = 0.477). We found no significant relationship between food delivery rate and the brood's average growth rate, even when controlling for adult group size and brood size (multiple regression model: *F* = 0.38, *P* = 0.325, brood size: *F* = -0.23, *P* = 0.821). We re-analyzed the data using only delivery rates of large prey items, but found no significant relationship (multiple regression model: *F* = 0.32, *P* = 0.772, adult group size: *F* = 0.21, *P* = 0.846, brood size: *F* = -0.22, *P* = 0.841).

Discussion

Our analyses did not detect a relationship between provisioning rates and nestling growth rates, even after we restricted analysis to the provisioning rate of large prey items, which was contrary to what we had expected. We expected nestlings fed at a higher rate would grow faster than those fed at a lower rate (Schwagmeyer and Mock 2008). Our index of prey item size (prey items were categorized based on relative size to beak) may not have

accurately reflected an important factor for growth: the nutritional content of prey items. Other factors, such as maternal investment in the egg (Russel *et al.* 2008), ambient temperature during growth, and the energy expended by nestlings through begging, were not considered and may be important for nestling growth as well (Rodriguez-Girones *et al.* 2001).

We tested the effect of adult group size on the frequency of food deliveries in joint nesting smooth-billed anis, and found evidence that members of larger breeding groups effectively reduced their individual provisioning work load. Because the frequency of nest visits was found to be highly correlated with the frequency of provisioning visits, our main results were not attributed to the frequency of food refusal by nestlings. This strategy, referred to as a compensatory or load lightening effect, usually occurs in helper-at-the-nest systems when nest success is limited by nest depredation (Hatchwell 1999), and may improve adult survivorship (Crick 1992). It has been observed in many species that breed cooperatively including purple gallinules (Porphyrula martinica; Hunter 1985, 1987), Florida scrub-jays (Aphelocoma coerulescens; Stallcup and Woolfenden 1978, Mumme 1992), pygmy nuthatches (Sitta pygmaea; Sydeman 1989), bicoloured wrens (Campylorhynchus griseus; Austad and Rabenold 1985), stripe-backed wrens (C. nuchalis; Rabenold 1984), grey-crowned babblers (Pomatostomus temporalis; Brown et al. 1978) and laughing kookaburras (Dacelo novaguineae; Legge 2000). Nestling growth rates were not related to adult group size, which is consistent with Loflin's (1983) findings in a population of smoothbilled anis in Florida, and illustrates how the amount of food nestlings receive is not

related adult group size, which is what we predicted would happen if anis adopted a compensatory or load lightening strategy. Our results are novel because they are the first to demonstrate a compensatory effect on provisioning in a plural joint nesting system.

Load lightening in cooperative species is generally though to reduce the risks and energetic costs associated with breeding (Brown 1978), which may increase survivorship (Crick 1992). Reducing individual nestling provisioning demands by living in large groups may be advantageous for adults for many reasons. Adults that spend less time visiting nests to provision young may spend more time at other activities, such as predator vigilance, territory defense, foraging and nestling brooding. In smooth-billed anis individuals take turns acting as sentinels, which alert the group when predators or intruders enter the territory. In Florida, larger groups of smooth-billed anis had sentinels in position for a higher proportion of time than small groups (Loflin 1983). Larger groups may also be able to spend more time incubating eggs or brooding young. In Taiwan yuhina, a joint-nesting passerine, the amount of time eggs were incubated increased significantly with adult group size, so that larger groups had a more even nest microclimate (Yuan et al. 2005). Inadequate nestling brooding may compromise nestling physiological processes such as digestion and growth (Dickinson and Weathers 1999), although it may not be as critical in species that nest where ambient temperatures are relatively high and constant, as is the case with smooth-billed anis in Puerto Rico. Group living has measurable advantages with regards to lightening the load of nestling provisioning, but may also reduce individual work load in terms of nest building, nest defense or other group activities (Crick 1992).

Although we found significant variability in the time intervals between food deliveries across ten nests, none of our measures of provisioning periodicity (coefficient of variation, maximum interval between feedings or average of five maximum intervals between feedings) were related to adult group size. Our results suggest that other factors, such as the synchronicity of food deliveries, which may be related to food availability in the territory or to the distance individuals have to travel to get food, may be more important than adult group size.

We have presented evidence that breeding in larger groups alleviates the individual contribution each adult makes to provisioning offspring in smooth-billed anis. Individual adults in larger groups provisioned significantly less frequently than those in smaller groups, even after controlling for brood size and nestling age. To our knowledge, this study is the first to demonstrate this effect in a joint nesting breeding system.

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a. Nestling provisioning frequency (total), model: F = 14.22, $r^2 = 81.1\%$, P < 0.001

	β coef	Т	Р
Constant	-2.835	-1.09	0.284
Adult group size	-0.0564	-0.21	0.835
Brood Size	1.7795	9.38	< 0.001

b. Nestling provisioning frequency (per capita), model: F = 12.92, $r^2 = 79.5\%$, P < 0.001β coef Т Ρ 1.60 Constant 1.1518 0.120 Adult group size -0.31742 -4.27 < 0.001 **Brood Size** 0.32697 6.23 < 0.001

c. Nestling provisioning periodicity (coef of var), model: F = 3.93, $r^2 = 49.4\%$, P = 0.072

	β coef	Т	Р
Constant	0.90056	3.41	0.011
Adult group size	-0.02081	-0.49	0.636
Brood Size	0.12574	2.76	0.028

d. Nestling provisioning periodicity (max interval), model: F = 1.14, $r^2 = 2.9\%$, P = 0.374 β coef Т Р 96.57 2.88 0.024 Constant Adult group size -8.368 -1.44 0.193 **Brood Size** 0.375 0.07 0.950

e. Nestling provisioning periodicity (average five max intervals), model: F = 0.54, $r^2 < 0.0\%$, P = 0.603

	β coef	Т	Р
Constant	45.52	2.99	0.020
Adult group size	-2.544	-0.96	0.397
Brood Size	-0.127	2.603	0.962

Table 2. Adult group sizes and parameters of the maximum time interval (max interval) and the average of five maximum time intervals (avg max interval) between feedings (mean, standard deviation and coefficients of variance [coeff of variance]) for ten video monitored groups.

Group ID	Group Size	Max Interval	Avg Max Intervals	Mean	Standard Deviation	Coeff of Variance
HO 02	6	49	28	9.5	11.1	1.2
4W 03	2	58	19	8.1	10.5	1.3
BI 03	6	52	27	5.6	9.5	1.7
HO 03	3	151	27	34.2	42.2	1.2
CB 04	3	47	69	26	19.4	0.7
NE 04	4	32	25	6.4	7.6	1.2
SF 04	8	34	33	4.4	5.8	1.3
4W 05	8	44	37	9.9	11.5	1.2
4W 07	4	69	42	4.7	9.7	2.1
MF 07	7	19	13	3	4.1	1.4

MSc Thesis – A Samuelsen McMaster – Biology

Figure 1. Bi-variate plot of delivery rates (items of food per hour) for the first three hours after nocturnal incubation versus delivery rates for the remaining (approximately seven) hours of daylight ($r^2 = 89.9\%$, F = 63.53, P < 0.001).



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Figure 2. Bi-variate plot of total delivery rate (items of food per hour) as a function of brood size (multiple regression model: F = 14.22, $r^2 = 81.1\%$, P < 0.001, adult group size: T = -0.21, P = 0.835, brood size: T = 9.38, P < 0.001).



MSc Thesis – A Samuelsen

McMaster – Biology

Figure 3. Bi-variate plot of per capita delivery rate (items of food per hour) as a function of brood size (multiple regression model: F = 12.92, $r^2 = 79.5\%$, P < 0.001, adult group size: T = -4.27, P < 0.001, brood size: T = 6.23, P < 0.001).



Figure 4. Bi-variate plot of total delivery rate (items of food per hour) as a function of adult group size (multiple regression model: F = 14.22, $r^2 = 81.1\%$, P < 0.001, adult group size: T = -0.21, P = 0.835, brood size: T = 9.38, P < 0.001).



MSc Thesis – A Samuelsen

McMaster - Biology

Figure 5. Bi-variate plot of per capita delivery rate (items of food per hour) as a function of adult group size (multiple regression model: F = 12.92, $r^2 = 79.5\%$, P < 0.001, adult group size: T = -4.27, P < 0.001, brood size: T = 6.23, P < 0.001).



MSc Thesis – A Samuelsen McMaster – Biology

Figure 6. Boxplot of time intervals (minutes) between consecutive feedings for nestling provisioning observations at ten video monitored nests, arranged randomly. Median (horizontal bar), interquartile range (shaded inner box) and range (outer box) shown.



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Chapter III

Future directions: Offspring recognition and discrimination in a joint-nesting cooperative breeder: the smooth-billed ani (*Crotophaga ani*)

Overview of offspring recognition and discrimination

Kin discrimination, the differential treatment of related and non-related individuals through recognition, appears in many social contexts, and is often employed when decisions that may improve an individual's reproductive success must be made (Waldman 1988). For example, adults can maximize their reproductive fitness when they direct parental care to their own offspring rather than non-related individuals (Trivers 1972, Beecher 1981, Waldman 1988, Clutton-Brock 1991), a phenomenon called offspring discrimination. Many invertebrates and vertebrates that provide parental care have developed the ability to recognize their own offspring, albeit to different degrees, and use this to discriminate against young that are not their own. Offspring recognition can be based on spatial or temporal information, in which case it is usually indirect, or can be based on physical or chemical traits of the offspring, in which case it is usually direct (Waldman 1988). Here, I present a brief overview of both indirect and direct offspring recognition, and relate this topic to attempted and future research on a communal cuckoo, the smooth-billed ani (*Crotophaga ani*).

For many species, adults rely on indirect evidence or "rules of thumb" to identify their young (Waldman 1988). Of course, recognition based on indirect evidence does not completely prevent adults from caring for non-related offspring; however, it should

increase the chances that adults allocate care to their own young (Waldman 1988). Indirect offspring recognition occurs in female burying beetles (Necrophorus *vespilloides*). In this species, the female's reaction to unrelated larvae is largely time dependent; she will only accept young that hatch at the same time that she expects her larvae to hatch. Müller and Eggert (1990) found that if unrelated burying beetle larvae were experimentally added to the host carcass on which a female had already laid eggs within the first hour after of her own larvae emerging, they were accepted by the female. However, if they were added before her larvae emerged, they were killed. Desert woodlice (Hemilepsitus reaumuri) also use a temporal cue for indirect offspring recognition (Linsenmair 1984). Females do not attack any new larvae for up to four to six weeks after they hatch, but will attack those that appear sooner than expected. In some vertebrates, spatial cues may be associated with offspring recognition. The location of a nest or burrow is often used as a means to locate offspring, in that any eggs or young present at the nest or burrow are accepted and cared for by parents. This usually occurs in situations when young are unlikely to intermingle. British storm-petrels (Hydrobates *pelagicus*), for example, provide direct care to any nestling present in their burrow (Mínguez 1997). California towhees (*Pipilo crissalis*) also use spatial cues to identify young indirectly. Adults of this species respond to distress calls of any fledglings that occur at or near the last known location of their young, and do not discriminate between calls of their own and unrelated fledglings (Benedict 2007).

The appearance of eggs or young and sound of young may be assessed by parents for recognition of offspring in birds. The relative size, shape, pattern or colour of eggs,

for example, may be important cues for hosts that have co-evolved with inter-specific brood parasites (Davies and Brooke 1989). African village weaverbirds (*Ploceus cucullatus*), for example, use differences in egg colour and speckling to discriminate the mimetic eggs of diederik cuckoos (*Chrysoccyx caprius*) from their own clutch, but do not use shape and mass (Lahti and Lahti 2002). Selection is strong in hosts that have coevolved with brood parasites; hence discrimination methods for these species have become very elaborate (Lahti and Lahti 2002). Anderson and Hauber (2008) suggest that differences in nestling begging calls may be used by parents to discriminate against unrelated nestlings and parasite nestlings.

When indirect recognition is not reliable, offspring recognition can become very refined. Offspring recognition is expected to be present in species where the costs and frequency of directing care to non-related young are high enough to select for recognition behaviours (*e.g.* development of highly individual sensory cues in young and sensitive perception in adults, Beecher 1991). Selection pressures for offspring recognition and discrimination are, therefore, expected to be strongest in systems where parental care, which is assumed to be costly to provide, must be directed to young that are aggregated with unrelated individuals. Adults of colonial-nesting birds are especially vulnerable to misdirecting parental care because nest sites are extremely close, making spatial cues non-existent or unreliable, and mobile young intermingle before they are independent (Beecher 1981). Many species of colonial-nesting seabirds tested to date do recognize and avoid caring for non-offspring, and some species even exhibit sex-biased differences in offspring recognition. Razorbills (*Alca torda*) have bi-parental care at the nest;

however, only males care for young after they fledge (Insley *et al.* 2003). Insley *et al.* (2003) found that offspring recognition abilities for males coincided with when young are mobile, but not yet independent, and are reliant on the male for parental care, whereas females that did not provide solo care showed no preference for their own young. Many species of bats that breed in large maternal colonies use the vocalizations of their pups to discriminate them from others in the colony (de Fanis and Jones 1996). Offspring recognition is a key adaptation to colonial living. Colonial-nesting seabirds, other colonial birds (*e.g.* cliff swallows *Petrochelidon pyrrhonota*) and bats have become model systems for the study of offspring recognition. Offspring recognition is also well developed in species that are hosts to inter-specific brood parasites as the costs and frequency of caring for parasitic nestlings are very high (Davies and Brooke 1989).

The mechanisms of offspring recognition vary and may relate to whether recognition is innate or learned. In some mammals, females appear to have an innate ability to identify their own offspring and are thought to do this by comparing the chemical signature produced by the young to their own (*i.e.* self-referent phenotype matching, Halpin 1991). Some recognition cues based on appearance, sound or smell are associated with learning. Experimental evidence has shown that adults in many colonial bird species learn to recognize the calls of their offspring through contact with them (*i.e.* recognition by association or prior association, Rothstein 1975), and that the onset of recognition often coincides with mobility of the young (Beecher 1991). In thick-billed murres (*Uria lomvia*) cross-fostered nestlings were accepted (*i.e.* were fed) by parents when they were swapped early (1-5 days old), were sometimes accepted when they were

swapped mid-way (6-13 days), but were always rejected when they were swapped late (14-22 days; Lefevre *et al.* 1998), illustrating the time it takes for parents to learn to recognize their offspring, which is based on selection for recognition and discrimination by the crucial age of mobility. In ancient murrelets (*Synthliboramphus antiquus*) parents were able to recognize precocious nestlings as soon as they were mobile, that is when young left their burrow at the age of only two days (Jones *et al.* 1987). Recognition is also important in communal species because multiple females share a breeding site. Degus (*Octodon degus*) are communal rodents that use familiarity of olfactory cues from urine and anal secretions to discriminate their own young from those of other females in the group (Jesseau *et al.* 2008).

Offspring recognition and discrimination in a joint nesting cuckoo

Joint nesting is an uncommon avian cooperative breeding system. A single nest is shared by a group of unrelated co-breeders, and adults cooperate to provide care for their altricial young until their independence (Quinn and Startek-Foote 2000, Vehrencamp and Quinn 2004). Just as in colonial birds, unrelated offspring of joint nesting birds intermingle; therefore, adults might benefit from being able to discriminate their own offspring so they could direct their care appropriately, thereby maximizing their own reproductive fitness. To our knowledge, no studies have tested whether adults can identify their own young in joint nesting birds. I propose that the smooth-billed ani, a joint nesting cuckoo, offers an interesting system with which both indirect and direct recognition and discrimination can be studied.

It has been suggested that egg tossing and egg burying, competitive behaviours observed in joint nesting birds such as smooth- and groove-billed anis (C. sulcirostris, Vehrencamp 1977), acorn woodpeckers (Melanerpes formicivorus, Koenig et al. 1995) and ostriches (tossing only, *Struthio camelus*, Betram 1979), may be products of egg recognition (Waldman 1988), and may ensure that laying is as synchronized as possible among females in a breeding group (Quinn and Startek-Foote 2000, Vehrencamp and Quinn 2004, Schmaltz et al. 2008). Females may be using an internal temporal cue: those that have not begun or are not ready to lay eggs would benefit from tossing or burying any other eggs in the nest, stopping only once they, themselves, have begun laying eggs. Alternatively, females may use indirect visual cues to identify the age of eggs. Freshly laid ani eggs are solid blue but coated with white calcite that scratches off as eggs are moved around the nest (Davis 1940). Moreover, egg size and shape vary with female identity (Chahine 2006). The ability of females to recognize their eggs may explain competitive behaviours in communal groups. Nestlings are also variable in size. Smooth-billed ani nestlings hatch asynchronously with anywhere from one to five days between the first- and last-hatched nestling (Quinn unpublished data). No studies have tested if eggs or nestlings have suitable cues for recognition or discrimination in a joint nesting bird, such as the smooth-billed ani.

I had originally planned to look at direct and indirect offspring recognition in a joint nester focusing specifically on nestling discrimination. I proposed to test whether adults directed parental care to their own offspring or to offspring that fell within the same size/age group as their own offspring using nest video monitoring data collected

from a population of smooth-billed anis in south-western Puerto Rico. Unforeseen complications with data collection did not permit me to do so. What follows is a brief account of said problems and a proposed course of action to allow future students or researchers to address these questions in smooth-billed anis or in another joint nesting species.

My first goal was to determine if there was evidence that adults could recognize nestlings directly. Nestling provisioning recordings were collected using video monitoring systems (Sandpiper Designs, Inc., Manteca, California) at Cabo Rojo and Laguna Cartegena National Wildlife Refuges (NWR) from 2002-2007. Cabo Rojo NWR is sub-tropical dry-forest and grassland bordered by farm- and pastureland, whereas Laguna Cartegena NWR has a fresh water lagoon at the base of the Sierra Bemerjas mountain range. For detailed descriptions of both field sites see Schmaltz et al. (2008). The population of smooth-billed anis at Cabo Rojo NWR has been monitored annually since 1998, whereas the population at Laguna Cartegena NWR was only monitored as needed, that is when groups were video monitored. Groups were censused about once a month (group size and identity of individuals recorded) throughout the breeding season (September to January) and as many adults as possible were captured using mist nets, funnel traps and nest traps each year. Whenever possible, adults were colour banded and given a temporary bill mark with non-toxic acrylic white nail polish to facilitate identification. Nests were located with behavioural observations and were monitored until nestlings fledged, approximately nine days after hatching. Of the twenty-two available, ten video monitored nests were selected, for which all video tapes were

reviewed to identify the nestlings and adults involved in each provisioning event. DNA extracted from blood samples from both adults and nestlings would allow me to determine if adults favoured provisioning their own offspring. Relatedness could be determined using microsatellite markers developed for smooth-billed anis (Blanchard and Quinn 2001).

Second, I wanted to determine if adults used the relative age or size of nestlings as an indirect cue to identify their own young. I planned an experiment to complement observational data collected from video monitoring nests. To see if adults use relative hatch date to indirectly discriminate young, I suggested the following manipulations on video monitored nests: 1) cross-foster 0-day old nestlings before expected hatch date and observe if adults feed or reject them, 2) cross-foster 0-day old nestlings at the same time others hatch, see if adults feed or reject, and 3) cross-foster 0-day old nestlings after others hatch, see if adults feed or reject.

I could not proceed any further than reviewing video tapes of unmanipulated nests. I could not execute cross-fostering experiment in 2007 because too few nests were found, and those that were used for another experiment. Moreover, I found that I could not use the footage I had of ten nests that appeared to be good candidates to address questions relating to direct nestling recognition. The biggest problem I encountered when reviewing video tapes was that I was not able to identify nestlings accurately, which made it impossible to see if adults were favouring certain young. Although nestlings were usually marked with non-toxic acrylic nail polish, I was only able to identify nestlings that had marks painted on their heads with white nail polish (one nest). Marks

made on wings, legs, back, and rump were not visible, and marks made with other colours, especially red and green, were difficult to see or differentiate. Because nestlings developed quickly, even the most visible marks wore off within two days, and nestlings were not always re-marked in time. I attempted following individual nestlings carefully to identify them using their relative location in the nest, but found there was too much uncertainty because nestlings were brooded for long periods, during which they appeared to move around under the adult. When I chose to look at size categories rather than specific individual nestlings, I found that relative nestling size was difficult to assess because camera angles varied and nestlings often appeared similar in size.

For many video monitored nests, it was also difficult to determine the identity of the adult at every visit. Although colour bands were helpful, full combinations were rarely observed because bands were hidden or colours unclear. From 2002 to 2006, adults were marked with a different pattern using non-toxic white nail polish, but because the marks were only on one side, they were not always visible from the camera's point of view. Starting in 2007, adults were marked with non-toxic white nail polish on both sides of their bill, which made them very easy to identify on screen.

Video-monitoring protocol

What follows is a summary of video monitoring guidelines that should be helpful for future researchers who wish to look at nestling recognition in smooth-billed anis or other joint nesting species.

- Nests selected for video monitoring of recognition and discrimination experiments should meet the following criteria: 1) group size during recording period is known, 2) all or most adults in group should be colour banded, although it would be best if all or most have white bill marks on both sides, 4) known hatch date and time for all nestlings, 5) measurements collected regularly for all nestlings (ideally at the same time of day) and 6) nestlings marked as described below.
- Nestlings should be marked clearly on the head with different patterns made with non-toxic acrylic white nail polish. Nail polish should be dry before nestlings are returned to their nest.
- 3) Position video camera so that nest contents and area around nest are visible so both nestlings and adults can be identified. Ensure that nest contents and adults are continuously visible and can be easily identified by checking not only with the field monitor at each nest visit, but by reviewing tapes on a larger screen between visits. Be prepared to adjust camera as necessary at every visit.
- 4) Minimize gaps in video footage by arriving at least one hour before tape is expected to end (23 hours after recording began), and check battery voltage with voltmeter every time tape is changed so that power does not run out unexpectedly. Keep nest visits as short as possible.

- 5) Nest checks should be scheduled as needed, but no more than two days apart to touch up nestling marks and get nestling measurements. Record time that researchers were present at the nest.
- 6) Avoid trapping adults and running non-related experiments and any other potentially disturbing activities at nests during video monitoring so that behaviours are not altered. If absolutely necessary, make sure to record time that observers were present and the activity.
- 7) Ensure video tapes are cared for properly so they last as long as possible. Store fully rewound tapes vertically in a cool dark place. Label tapes carefully, with the following information: 1) year, 2) letter that identifies nest, 3) territory, 4) date, and 5) start and finish times. Annotate any interesting behaviours as they are encountered in video inventory.

The mixed-parentage broods of joint nesting birds are an interesting and unexplored system with which offspring recognition can be studied. In many ways, joint nesters are similar to colonial-nesting birds and hosts that have co-evolved with brood parasites, in which offspring recognition is well developed; therefore, we expect to observe some degree of nestling discrimination. Variation in both egg and nestling characteristics suggest there is potential for studies of both direct and indirect recognition and discrimination in this species. Although this attempt to investigate nestling recognition and discrimination in smooth-billed anis was unsuccessful, I believe it will be possible in the future if the recommendations suggested in this chapter are considered.

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