TERRITORY QUALITY IN THE SMOOTH-BILLED ANI

AN INVESTIGATION OF TERRITORY QUALITY IN THE SMOOTH-BILLED ANI (*CROTOPHAGA ANI)*

By

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Abstract

Territorial behaviour is exhibited in cooperative breeders. The quality of defended territories can vary, and high-quality sites, which enhance fitness, should be used preferentially over poorer-quality sites. This study was intended to address issues of territory quality within the plural breeding, joint-nesting, smooth-billed ani (*Crotophaga ani*). I tested the communal joint-nesting threshold hypothesis, which posits that independent pairs will pay the price of group living if compensated by acquiring a superior territory. My results quantified differences in territory quality in terms of time of first breeding and chances for re-nesting or second-brooding. Per capita territory quality correlated negatively with group size, in conflict with the communal joint-nesting threshold hypothesis.

Another hypothesis to explain communal behaviour is the habitat saturation hypothesis. This postulates that offspring remain in their natal territory and delay reproduction because of a local absence of suitable breeding habitat. I tested the habitat saturation hypothesis, which was developed to explain the evolution of group living in cooperatively breeding birds. I compared occupied ani territories with vacant sites, using eight ecological variables that may be important to the fitness of a group. In addition, I compared occupied territories with sites that were occasionally occupied. I did not find the habitat of our population of smooth-billed anis to be saturated. Some sites were never occupied because there are territory characteristics that presumably limit breeding. In contrast with expectations of habitat saturation, there were suitable sites available for breeding that were not in use. Results from both hypotheses presented suggest that there are not obvious group-living benefits and that one must consider other explanations for the evolution and maintenance of this system.

Preface

This thesis contains four chapters. The first chapter is a general introduction, and the forth chapter contains general conclusions and future directions. Chapters two and three are in preparation for submission to the journal *Behavioral Ecology*. Information about the title, authors, and individual contributions to each of the chapters is outlined below:

Chapter 2: "Testing the 'communal joint-nesting threshold' hypothesis in the plural-breeding smooth-billed ani (*Crotophaga ani)*: territory quality and group size"

> Authors: C. Lentz, G. Schmaltz, and J.S. Quinn
> Contribution: Field work including capturing, banding, and transmitting anis, identifying territory boundaries, and arthropod sampling were preformed by the candidate with assistance and direction from G. Schmaltz and J.S. Quinn. Telemetry sessions and vegetational characterization were performed by the candidate and various field assistants. Rain data were provided by US Fish and Wildlife Services. Data entry and analyses in ArcView 3.2 were performed by the candidate with guidance from A. Johnson and G. Schmaltz. Statistical analyses were conducted by the candidate with guidance from J. Stone (path analysis) and A. Musters. The manuscript was written by the candidate with suggestions and guidance from J.S. Quinn. The research was conducted under the supervision of J.S. Quinn.

Chapter 3: "A test of habitat saturation in the plural-breeding smooth-billed ani (*Crotophaga ani*)"

> Authors: C. Lentz, G. Schmaltz, and J.S. Quinn
> Contribution: Field work including capturing, banding, and transmitting anis, identifying territory boundaries, collecting nest data, and arthropod sampling were preformed by the candidate with assistance and direction from G. Schmaltz and J.S. Quinn. Telemetry sessions and vegetational characterization were performed by the candidate and various field assistants. Ecological variables were measured by the candidate. Unoccupied sites were identified by the candidate with assistance from G. Schmaltz and J.S. Quinn. Statistical analyses were conducted by the candidate with guidance from A. Musters. The manuscript was written by the candidate with suggestions and guidance from J.S. Quinn. The research was conducted under the supervision of J.S. Quinn.

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CHAPTER 1

General Introduction

GENERAL INTRODUCTION

Most bird species breed as monogamous pairs, building a single nest in which they raise their own young (Lack, 1968). Some species breed in communal breeding systems, where helpers feed and care for non-filial young. Such systems are quite rare - only about 3% of bird species are communal breeders (Emlen, 1997). The benefit of helpers, and/or additional group members, is commonly attributed to increased group fitness, such as higher survival rates and increased reproductive success (Brown, 1978). Communal species live in groups of between 2 and 20 members, with individuals cooperating to defend all-purpose territories, build nests, and care for young (Brown, 1978). Members of the group tend to stay together during regular activities, such as roosting, foraging, and resting. Some confusion has arisen in the distinction between the terms communal breeding and cooperative breeding. Early definitions were not synonymous (Lack, 1968), but, more recently, they have been used interchangeably.

Types of communal breeding include helping-at-the-nest systems (non-breeding offspring delay dispersal and remain on their natal territory) and various forms of cooperative polygamy or plural breeding systems (more than a single male or female breed within the same social unit and nest). Helper-at-the-nest systems have been documented in species such as the Florida scrub jay (Woolfenden, 1975), long-tailed tit (Gaston, 1973), and red-cockaded woodpecker (Ligon, 1970). The more complex and rarer joint-nesting plural-breeding system includes more than one breeder in a group with breeding females laying eggs in the same nest. Occasionally, groups contain non-breeding helpers or offspring from previous years. In some joint-nesting species, the females compete by tossing and burying eggs suspected of belonging to others, but, then, later distribute nestling provisioning evenly among the adults (Vehrencamp and Quinn 2004). Brown (1978) suggested that competition within a group is expected to involve a battle for breeding status. Thus, there is individual rivalry within each unit (a social group that feeds, roosts, and nests together) combined with a determination to remain as a unit for group-living benefits. This system has been described in species such as the acorn woodpecker (Koenig, 1981), the Mexican jay (Brown and Brown, 1990), the pukeko (Craig, 1979), the yuhina (Yuan et al., 2004; Yuan et al., 2005), the groove-billed ani (Vehrencamp, 1978), and the smooth-billed ani (Davies, 1940; Loflin, 1983).

The evolution of communal breeding has been attributed to ecological constraints (Emlen, 1982). These constraints include high cost (risk) of dispersal and establishment of a suitable territory, shortage of high quality breeding territories, and shortage of sexual partners. Because of these limitations, young individuals that are capable of breeding remain on natal units and may serve as helpers. Emlen (1982) suggested that helpers benefit from delayed reproduction by gaining experience, maturity, indirect genetic benefits by raising young that are close relatives, as well as increasing chances of survival. Ecological constraint models have been tested in both helper-at-the-nest systems

(Komdeur, 1992; Zack and Ligon, 1985; Woolfenden and Fitzpatrick, 1984) and in joint-nesting systems (Macedo and Bianchi, 1997; Koford et al., 1986).

Most communal species engage in territorial behaviour. Groups reside in a specific area of habitat and defend it against other individuals of the same species. Wilson (1975) defined a territory as, "an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defence or advertisement". Choice of territory is an important decision for prospecting individuals. In communal birds, territories can differ in prey availability, number of nesting and roosting sites, tree density, and other ecological variables, all of which may be important to the fitness of the group. Polygynous, polyandrous and communal breeding systems may have evolved on the basis of territory quality variation. Under some circumstances, an individual or pair will gain more by mating on a high quality territory already occupied by an individual (male, female, pair, or group) than in a monogomous pair on a low-quality territory. If individuals are compensated for the cost of sharing with high-quality resources, they may choose to settle on a territory that is already occupied. This idea was first presented by Orians (1969) as the polygyny threshold model and was originally suggested to explain the evolution of polygynous systems. The model has since been applied more broadly than originally presented (Gowaty, 1981; Davies, 1989) and generalizations of the model are used beyond its original intent.

Various methods have been used to measure territory quality, but the critical territory factors identifiable to birds are not always known by researchers. Prey availability and structural or floristic characteristics have been used as territory quality measures (Hunt, 1996; Braden et al., 1997; Komdeur, 1992). Measures of food availability have been offered as the most direct assessment of quality for particular species, but some research suggests that it is difficult to accurately measure usable resources (Luck, 2002). Poulin et al. (1992) addressed this challenge in a study of avian breeding activity in relation to food resource abundance and food exploitation by birds in Venezuela. After capturing birds and forcing regurgitation, their diet was determined. Arthropod abundance was evaluated using four different trapping methods: light trap, pitfall trap, malaise trap and sweep-netting, with conclusions that the sweep-net method best represents the types of prey eaten by insectivorous birds, and can be used as an accurate measure to assess prey availability. Canopy cover has also been offered as a general measure of territory quality in birds because this variable is important for protection, nesting opportunities, and roosting opportunities (Koford et al., 1986). Some territory quality indices may be species-specific. In the acorn woodpecker, the number of storage holes available was used as a territory quality index (Stacey and Ligon, 1987). Acorn woodpeckers store oak and pine mast in specially modified storage trees or granaries. Storage mast is a valuable food resource in winter and the total amount available on a territory depends on the number of holes available for storage. The number of storage trees had a significant effect on survival and reproductive success of individuals occupying that territory and was, therefore, used as a territory quality index (Stacey and Ligon, 1987). Because individuals on high-quality sites will potentially have the highest fitness, all territory quality measures used should correlate with fitness to ensure accuracy (Koford et al, 1986).

The purpose of this thesis was to test various hypotheses regarding the relationship between territory quality, group size, reproductive success, and timing of reproduction in the plural breeding, joint-nesting, smooth-billed ani (*Crotophaga ani).* Both hypotheses investigated the evolution and maintenance of communal behaviour. Territory quality was evaluated to determine if benefits associated with high-quality territories outweigh the costs of group-living. Territory quality, using specific ecological variables, was evaluated in occupied and unoccupied territories to identify which ecological variables may be important in territory choice.

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CHAPTER 2

Testing the 'communal joint-nesting threshold' hypothesis in the plural-breeding smooth-billed ani (*Crotophaga ani)*: territory quality and group size

ABSTRACT

Here we propose and test a modified version of the polygyny threshold hypothesis as applied to socially monogamous, plural breeding, joint-nesting, smooth-billed anis (*Crotophaga ani)*. The Polygyny threshold model addresses territory quality and mate choice by proposing that females will pay the cost of polygyny if compensated by obtaining a superior territory. Here we test a new modification called the communal joint-nesting threshold hypothesis which posits that independent pairs will pay the price of group-living if compensated by acquiring a superior territory. Ani groups actively defend territories that vary in quality. Group membership includes such costs as energy and risk associated with territory defence and competitive losses due to egg tossing and burial by other group members. Individuals or pairs should balance the quality of available territories against the costs of group membership when deciding where to breed. Territory quality may change during the breeding season and our results show that individuals shift foraging patterns to coincide with the prey-richest vegetation type during the peak and late periods of the breeding season. Territories with a larger proportion of guinea grass allowed earlier breeding starts and may afford greater re-nesting opportunities following a failure or second-brooding opportunities. Territory quality, estimated based on per capita prey availability, was correlated positively with per capita fledging success. However, group size was correlated negatively with per capita fledgling success.

Territory quality per capita also correlated negatively with group size and together these results are inconsistent with the communal joint-nesting threshold hypothesis. Per-capita reproductive and territory quality attributes do not favor group-living. We suggest that social and longevity advantages maintain group-living. *Key words: Crotophaga ani*, joint-nesting plural-breeding, polygyny threshold model, territory quality, reproductive success, reproductive timing.

INTRODUCTION

Cooperative breeding occurs when adult group members contribute care to non-filial young. In birds, many such species have a despotic "helper-at-the-nest" system. Young individuals remain in their natal unit, delaying their reproduction, and help raise relatives (Brown, 1978). In a few species, more than one breeder exists in a group (plural breeding) and more than one female lays eggs in the same nest (joint-nesting) (Vehrencamp and Quinn, 2004). The group cooperatively cares for the mixed clutch (Brown, 1978).

Territorial behavior is exhibited in cooperative and joint-nesting breeders and occurs when a social unit actively defends a territory from conspecifics (Gordon, 1997). The size of a defended territory may be related to the abundance of prey available to the birds (Smith and Shugart, 1987). The quality of these defended territories can vary, and high-quality sites, which enhance fitness, should be used preferentially over poorer-quality sites (Luck, 2002). Fledgling success (the number of surviving young per breeding season) is correlated with territory quality in joint-nesters (MacRoberts and MacRoberts, 1976; Langen and Vehrencamp, 1998; Craig, 1979). Survival, an additional fitness component, may also be influenced by territory quality (Komdeur, 1992; Luck, 2002; Braden et. al., 1997; Matthysen, 1990).

Territory quality varies with a number of ecological variables within the territory, some of which are sensitive to seasonality. To maximize fitness, a group should breed on the best territory available at the most suitable time for breeding. In tropical habitats with sharply defined wet and dry seasons, birds typically time the breeding phase of greatest need to coincide with annual peaks in food availability, when predictable (Perrins, 1970; Martin, 1987; Jetz et al., 2003). Although rain may be predictive of food availability, little is known about the exact cues that stimulate reproductive activity (Hau, 2001).

Many studies of territorial species, including joint-nesters, have attempted to measure territory quality (Macedo and Bianchi, 1997; Koford et al., 1986; Komdeur, 1992), but there has been debate about whether the most appropriate measure of territory quality is food abundance or structural characteristics, such as tree density. Koford et al. (1986) suggested that the most straightforward indication of the quality of a certain area is the fitness of the individuals living there and found that tree area was the ecological variable most correlated with fitness in a study of groove-billed anis (*Crotophaga sulcirostris).* Other studies showed that the abundance of invertebrate prey is positively correlated with preferred structural characteristics, suggesting that assessment of food abundance for insectivores is the most meaningful representation of habitat quality (Smith and Shugart, 1987; Luck, 2002). Food availability is tightly linked to individual fitness (Lemon, 1991; Jetz et al., 2003).

To improve fitness further, individuals should choose high-quality mates. Females can gain both direct and indirect benefits from mate choice and should be selected to optimize their choice based on several different cues (Zuk et al., 1990; Qvarnström et al., 2000). The most common avian mating system is based on resource defence, and experimental studies have shown that, in some species, females base their choice of social mate entirely on the quality of the resource defended (Alatalo et al., 1986; Pärt, 1994). The polygyny threshold model (Orians, 1969; Verner and Willson, 1966) addresses territory quality and mate choice, positing that, under some circumstances, a female will gain more by mating with an already mated male with greater resources than with a single male with poorer resources. This model applies to species in which the territory of a male contains useful resources for the female and her offspring. Choice of an already-mated male can be advantageous if the female is compensated for the cost of polygyny by obtaining a sufficiently higher quality territory (Verner, 1964; Orians, 1969). This model has been used to predict the ecological conditions under which we would expect avian resource defense polygyny to evolve (Orians, 1969). The Polygyny threshold model has since been expanded to explain other variations of mating systems, including the evolution of cooperative polyandry (Gowaty, 1981; Davies, 1989). We propose an additional expansion of the model to address the communal joint-nesting breeding system.

The smooth-billed ani (*Crotophaga ani)* is a joint-nesting, plural-breeding member of order Cuculiformes. Members of ani groups are usually unrelated but occasionally include mature offspring that failed to disperse. Individuals form socially monogamous pair bonds and cooperate as a group to incubate eggs, care for nestlings, and defend territory (Quinn and Startek-Foote, 2000). Adults also engage in competitive behaviors such as egg tossing and egg burial. In some species of joint-nesters, including smooth-billed anis, individuals typically disperse from their natal territory and either join an already existing group or form a single breeding pair. Prospecting individuals or social pairs must join a group on an already occupied territory, presumably of high quality, or settle on a vacant territory of lower quality. This sets the stage for a modification of polygyny threshold model that we call the communal joint-nesting threshold model. This posits that independent individuals or pairs will pay the cost of group-living if compensated by acquiring a superior territory. Assumptions of the modified model include the following: (1) groups defend territories varying in quality which influences reproductive success; (2) there is a cost to individuals or pairs of sharing a territory; (3)

individuals can assess territory quality and/or group size and survey available opportunities; and (4) individuals or pairs are free to settle where their expected reproductive success is greatest. We have evidence supporting each of these assumptions.

Here we examine the interactions between smooth-billed ani territory quality as related to group size, timing of breeding, and breeding success. This background provides the basis for the primary objective of this study, which is to test the communal joint-nesting threshold hypothesis. We hypothesize that prospecting anis are settling on already occupied territories of higher quality if compensated for costs of group-living, as predicted by the communal joint-nesting threshold model. We predict that groups on the highest quality territories will have the most members, which can be confirmed with a positive correlation between territory quality and group size. We further predict that groups on higher quality territories will have a higher per capita reproductive success.

METHODS

Study area

We studied smooth-billed anis in southwest Puerto Rico on the Cabo Rojo National Wildlife Refuge (17°59'N. 67°10'W) and surrounding properties. The study area was approximately 2 x 2 km. The habitat in our study area was a combination of treed grassland, with areas of riparian forest, surrounded by farm fields and rural residential areas.

Species and study population

The smooth-billed ani is a plural-breeding, joint-nesting species. Groups contain from 2 to 17 or more adults. Breeding activity is greatest during the rainy season, and some groups raise more than one brood. During the dry season, territories tend to break down and many groups will join together and forage as a large flock (Quinn and Startek-Foote, 2000). Smooth-billed anis thrive in disturbed areas where open spaces are created, such as secondary succession agricultural and residential zones (Quinn and Startek-Foote, 2000). Anis in this area nest predominately in thorny tress, such as Mesquite (*Prosopis juliflora*) and Rolon (*Pithecellobium dulce*).

General field methods

Our goals were to quantify territory quality, group size, reproductive success, and the timing of breeding. Data reported here were predominately collected from September 2003 to January 2004 and from September 2004 to January 2005. These dates coincide with the rainy season and peak breeding activities of the smooth-billed ani.

We captured anis using mist netting, funnel trapping with lure birds, and nest trapping (Mock et al., 1999). We took standard measurements and a small blood sample from each individual captured. We attached a 2.1g transmitter (Holohil Inc.) to a single healthy individual from each group whenever possible. We engaged in 2-hour telemetry sessions every three to four days as long as the transmitter remained in-tact to follow the transmitted bird and associated group members that tended to remain together for daily activities. We collected the following data: group size, group locations, nest sites, and foraging patterns. We performed an average of 8.75 ± 1.05 SE telemetry sessions on each transmitted bird (range 2-15). The number of sessions performed was variable, due to the variation on the length of time the transmitter remained on the bird. Some transmitters fell off and were found within a week of being attached, while others remained on the bird for several months. We discontinued sessions if the signal from the transmitter could not be detected.

We determined territory boundaries for each group on the study site in two ways. First, we marked locations of groups encountered during routine outings on a map and second, we recorded the group's GPS (Global Positioning System) coordinates during telemetry sessions. We transferred locations for each group to ArcView 3.2 and enclosed the location points with straight lines to form a polygon that defined the total area of utilized territory.

Each year, we identified and named groups in the study area according to their location, so that after several years, many groups were assigned the same name even though they were not the same group with regards to number and group membership. For this reason, we considered each group for separate years of the study, an independent group. To confirm this, we calculated a proportion of shared dyads from 2003 and 2004. We calculated the proportion of shared dyads (P_{sd}) as,

$$P_{sd} = \frac{2\left(\sum_{x=1}^{s} (s - x)\right)}{\left(\sum_{x=1}^{A} (A - x)\right) + \left(\sum_{x=1}^{B} (B - x)\right)}$$

where *s* is the number of shared dyads, *A* is the total number of dyads in the group for year 1 and *B* is the total number of dyads in the group for year 2. Using this equation, we were able to establish the degree to which groups retained the same adult membership and/or group size. The two elements, group composition and group size, can be illustrated by the following two examples. Group size changed on the North House territory from twelve individuals in 2003 to five in 2004. All 5 of the 2004 individuals had been present on the territory in 2003. P_{sd} accounts for the difference in size between years despite the fact that five members were retained. P_{sd} for this group was calculated to be 0.263. In the second example, group size in the Casablanca group remained consistent between years, but group membership did not. All three members in 2003 were not present in 2004, and three new members moved into the territory. P_{sd} for this group was calculated to be 0.00. This index accounts for both group size changes and changes in group membership. Using the banded individuals in our study population (51% of adults in 2003 and 53.5%

in 2004), an average proportion of 0.064 ± 0.036 SE was found for the groups in our study area (Range 0 – 0.333), indicating that, on average, 6% of the individuals in the group remained from one year to the next. Therefore, we treated the data for each group-year as independent.

In 2003, we sighted 25 adults banded in previous years. Our research team banded 20 new adults and 40 chicks using one U.S. government issued aluminium band and 3 color bands of differing combinations. An estimated 51% of the total 89 adults present in the study area were banded by the end of the 2003 breeding season. We fitted eight of these adults from eight different groups with a transmitter. In 2004, we sighted 24 adults banded in previous years. Our research team banded 37 new adults and 59 chicks, and transmitted 11 of these adults from 10 different groups. An estimated 53.5% of the total 114 adults present in the study area were banded by the end of the 2004 breeding season.

Monthly rainfall data were collected by local US Fish and Wildlife Services during the study period (Figure 2.1) using a USGS (United States Geological Survey) weather station that is a part of SCAN (Soil Climate Analysis Network). Data were compiled from the USGS station and from manual readings on the local rain gauge.

Prey abundance and territory quality

Smooth-billed anis forage almost exclusively on insects and spiders in grassy and herbaceous vegetation therefore sweep-netting was used to evaluate prey abundance. This method was found to be the most accurate method to represent the types of prey eaten by ground feeding insectivores (Poulin et al., 1992).

Four vegetation types dominated our study area: buffel grass (*Centris ciliaris),* hurricane grass *(Fimbristylis spathacea)*, guinea grass (*Panicum maximum)* and a lantana (*Lantana involucrate).* On three occasions during each breeding season we took sweep samples at 27 locations for each of the four different predominant vegetations in the study area (108 sampling locations in total).). The foraging data we collected from telemetry sessions supports this decision, as 94.5% of all recorded foraging minutes were spent in buffel grass, guinea grass, hurricane grass, or lantana. The other 5.5% was accounted for in trees, vines, berry bushes, and other grass species. Sampling occurred as follows: October 14-16 (early), Nov 28-29 (peak), and January 4-6 (late) in 2003 and October 9-10, November 20-21, and January 3-4 in 2004. Sampling at each site required 25 steps with one vigorous sweep of the net made for every step taken, and each step being about one meter. We quantified the 27 samples for each vegetation type from around the study area and determined average arthropod abundances for each vegetation and sampling period (early, peak, late). We recorded sampling locations as GPS coordinates so that the same patch of vegetation could be used each sampling period. We sun-dried all arthropods for a total of 24 hours and calculated biomass (g dry weight/25 sweeps).

We determined the total area of predominant vegetation by using an aerial photograph as a guide and confirming all patches of vegetation by ground-truthing. We transferred the map in to ArcView 3.2 and determined the area of each vegetation type for each territory. We used Komdeur's (1992) territory quality index (TQ) that is based on prey availability, calculated as

$$TQ = (a \sum_{x=1}^{4} (c_x i_x))/100$$

where a is the territory size, c_x is the proportion of area covered by vegetation type x in a given territory, and i_x is the prey abundance (g dry weight/25 sweeps) for vegetation type x. Using this equation, we determined quality, in terms of prey abundance, for each territory in our study site three times (early, peak, and late) during the breeding season. We used an average of these three calculations for an overall territory quality.

Data analysis

We did not collect complete information for all groups (Table 2.1). We excluded groups from the certain analyses if the entire territory was not accessible (many territories include private property in which access was not available). We also excluded groups if time limitations prevented opportunistic sightings and if data was insufficient to establish good estimates of territory boundaries (some groups were on the perimeter of the study site and were followed occasionally). For these groups we did not have reliable estimates regarding their territory size, group size, or reproductive success, so they were excluded from certain analyses.

We tested relationships among territory quality, group size and reproductive success with Spearman rank correlations. We monitored group size, the total number of adults capable of breeding in a group, regularly throughout the breeding season. We measured reproductive success for each group as the total number of young in a season that were sighted after leaving their nest tree. These fledged young had the ability to fly, glide, or flutter from tree to tree. We used an average of the three territory quality values calculated (early, peak, late) as overall territory quality. We calculated canopy cover for each territory using an aerial photo in ArcView 3.2 and correlated canopy cover with reproductive success.

We examined the relationship between territory quality, group size and reproductive success from an absolute and a per capita basis. We defined per capita reproductive success as the total number of fledged young divided by the number of adult individuals in the group. We also calculated and analyzed territory quality on a per capita basis ($TQ_{(per\ cap)}$) using the following modified equation from Komdeur (1992):

$$TQ_{(per\ cap)} = a_{pc} \sum_{x=1}^{4} (c_x i_x)$$

where a_{pc} is the territory area divided by the number of adults in the group, c_x is the percent area of vegetation type x, and i_x is the prey abundance for vegetation type x.

To help clarify mutual interactions among the three main parameters, group size, territory quality and reproductive success, we used a path analysis. Path analyses decompose inter-variable relationships into direct causes (i.e., territory quality on reproductive success and group size on reproductive success). Path analyses are models depicted as path diagrams. The general equation for a chain in a path diagram is

$$r_{1y} = p_{Y1} + r_{12}\, p_{Y2}$$

where r_{1y} (total effect) is the Pearson correlation coefficient between X_1 (first predictor variable) and Y (criterion variable), p_{Y1} (direct effect) is the standardized partial regression coefficient of X_1 and Y, r_{12} is the Pearson correlation coefficient between X_1 and X_2 (second predictor variable), and p_{Y2} is the partial regression coefficient of X_2 and Y. The product of r_{12} and P_{Y2} represents the indirect effect. Path diagrams also involve an unknown variable, *U*, as, in most cases, one does not know all the factors that explain the variation of a dependent variable (Sokal and Rohlf, 1995; Figure 2.2). Path analysis reduces to multiple regression under the assumption that predictor variables are independent causes of the dependent variable. In the path analysis presented herein per capita territory quality is used as X_1, group size as X_2, and per capita reproductive success as Y (Figure 2.3).

We correlated the percent time foraging in a specific vegetational type with prey abundance of the respective vegetation to see if individuals shift their foraging patterns to the most productive vegetation with respect to prey abundance. We recorded foraging time per vegetation type during the 2-hour telemetry sessions. We divided sessions into early, peak, and late season and tallied foraging time in each vegetation type. We tested for a correlation between the percentage of time spent in the different vegetation types and the relative prey abundance of each vegetation type during each sampling period. We used the relative prey abundance instead of absolute prey abundance to take into consideration that all grasses had low prey availability during dry periods.

Although rain patterns were generally consistent throughout our study area, breeding times differed among groups, some breeding early, some breeding late, and others breeding more than once throughout the breeding season. We performed several correlations to determine which variable(s) explained the timing of breeding. Each day of the field season was assigned a number beginning with September 1 as day 1 and ending with January 18 as day 140. We determined the day to when incubation began, the date of first detection of the eggs being warm after clutch completion, for each group. We carried out checks on active nests every other day so incubation dates were within two days. We excluded nests found after incubation began from the analysis. We used incubation start dates to define breeding time because the duration of egg-laying varied with group size and not all clutches of eggs survived until hatching. We expected territory quality to affect the timing of breeding and therefore predicted early reproduction of groups on high quality territories. As well we expected group size to influence the timing of reproduction. Smaller groups have a shorter egg laying period because fewer females lay their eggs in the nest and competitive behaviors in smaller groups are less evident. We also analyzed territory composition, percent of the four vegetation types sampled for prey availability, in terms of timing.

Statistics

All data analyses were conducted using the software package SAS 9.1.2 (SAS Inc.). The presented probability values are two-tailed with an alpha level set at 0.05. Hereafter means are presented with standard error.

RESULTS

Study population and breeding activity

In this study population, ani breeding group sizes averaged 5.3 (± 0.59, $n = 34$) and ranged from a pair to 17 birds. The most common group size observed was 3 individuals (29.4%), with the next most common group size being 5 individuals (14.7%) (Table 2.1).

Rainfall in south-western Puerto Rico is highly seasonal, falling mostly between the months of August through December (wet season). Annual rainfall in 2003 was 2242.8mm with 86.3% of the rain falling during the wet season. Annual rainfall in 2004 was 746.8mm with 55.8% of the rain falling during the wet season (Figure 2.1). The yearly average for the region is 919.5 mm. The number of active nests was greatest in November and December in 2003 and greatest in November in 2004 (Figure 2.1).

Timing of reproduction and foraging patterns

Percent guinea grass in a territory negatively correlated with the date incubation begins ($r = -0.531$; $n = 22$; $p < 0.025$). Territory quality, group size, percent buffel grass, percent hurricane grass, and percent lantana did not correlate with the start of incubation (Table 2.2).

Spearman rank correlations showed a non-significant trend for individuals to shift their foraging efforts to the most prey-rich vegetation ($r = 0.427$; $n = 20$; $p = 0.06$). Specifically, anis preferred the prey-richest vegetation during the peak ($r = 0.785$; $n = 8$; $p < 0.025$) and late ($r = 0.771$; $n = 8$; $p < 0.05$) seasons but not during the early breeding season ($r = -0.400$; $n = 4$; $p = 0.600$). The early breeding season had only 4 observations (2004 data) because we had not yet placed transmitters on any adults during the early breeding season in 2003. Consequently, telemetry sessions were not carried out and foraging data were not collected.

Territory quality, group size, and reproductive success

Per capita reproductive success was positively correlated with per capita territory quality (Spearman rank correlation: $r = 0.6581$; $n = 26$; $p < 0.001$). However, per capita territory quality was negatively correlated with group size (Spearman rank correlation: $r = -0.5801$; $n = 26$; $p < 0.01$). We found no relationship between canopy cover and reproductive success (Spearman rank correlation: $r = 0.102$; $n = 26$; $p = 0.617$). Larger groups did not occupy larger territories with more prey available (Spearman rank correlation: $r = 0.347$; $n = 26$; $p = 0.08$). However, larger groups occupied territories with larger areas of guinea grass (Spearman rank correlation: $r = 0.462$; $n = 26$; $p < 0.025$). Group size also correlated with prey availability in guinea grass (estimating the amount of prey in all guinea grass on territory) during the early (Spearman rank correlation: $r = 0.449$; $n = 26$; $p < 0.025$) and peak (Spearman rank correlation: $r = 0.448$; $n = 26$; $p < 0.025$) sampling periods, but not during the late sampling period. Reproductive success (total number of fledged young per group) showed no relationship with group size (Spearman rank correlation: $r = -0.0145$; $n = 34$; $p = 0.933$) and we found a significant negative relationship between per capita reproductive success and group size (Spearman rank correlation: $r = -0.401$; $n = 34$; $p < 0.025$).

We tested the hypothesis that per capita reproductive success is affected directly by per capita territory quality and indirectly by group size, using path analysis (Figure 2.3). The overall model was significant ($r^2 = 0.472$; $p < 0.001$). The Pearson correlation coefficient between territory quality (per capita) and reproductive success (per capita), or total effect, (0.6397) was equal to the sum of the indirect effect (0.1218) and the direct effect on per capita reproductive success (0.5178); as the r value approximates closely the actual Pearson correlation, the path analytic model seemed to be appropriate.

DISCUSSION

Examination of the communal joint-nesting threshold model requires an accurate assessment of territory quality. Many studies have attempted to measure territory quality, but it is difficult to assess critical territory factors that influence reproductive success in birds (Vehrencamp, 1978). We estimated prey abundance as an index of territory quality (Komdeur, 1992). Because high quality sites enhance fitness (Luck, 2002), we predicted a positive relationship between territory quality (per capita) and reproductive success (per capita). The positive relationship we found between these variables led us to two conclusions. First, we used an appropriate measure of territory quality for this species, and second that the assumption of the communal joint-nesting threshold model was met: groups defend territories varying in quality, which influences reproductive success. Canopy cover has also been offered as a measure of territory quality because it is important for protection, nesting opportunities and roosting opportunities (Koford et al., 1986). In a study on groove-billed anis Koford et al. (1986) used canopy cover as territory quality because they showed that anis preferentially selected areas with relatively high percent tree cover and such areas were limited in their study site. Because there was typically sufficient canopy cover on all territories in our study area, we would not expect additional canopy cover to dramatically increase fitness, especially given that foraging habitat for the smooth-billed ani is not usually under canopy. Moreover we found no relationship between canopy cover and reproductive success, and therefore, did not use canopy cover as a measure of territory quality.

We predicted that larger groups would have larger territories with more prey available, but failed to show a significant effect. This finding suggests the possibility that high densities of prey may be more important than overall prey availability. Interestingly, larger groups have territories with greater areas of guinea grass. The amount of prey available in guinea grass for each territory correlated with group size, suggesting that guinea grass is a valuable resource and important contributor to territory quality in our study area.

We found that territory quality alone explained significant variance in reproductive success. The path analysis further explained this relationship by showing that territory quality influenced reproductive success primarily through a direct effect. This exploratory analysis showed that group size is an additional factor indirectly influencing reproductive success and together with territory quality a significant portion of variance was accounted for. Other variables that we did not measure must have also contributed to reproductive success, as 100% of the variance was not accounted for.

Territories were found to have a broad range of quality values (Table 2.1). Quality differed between groups and changed through the breeding season. Seasonal shifts in territory quality occurred in our study, with the period of greatest prey abundance occurring during the peak periods of each season. High-quality territories extended to the late period of the 2003 field season (due to the high levels of rainfall) but the late period of the 2004 season became dry and unproductive with the majority of territories becoming low in quality (Table 2.1). Despite the different climate conditions in 2003 and 2004, qualitative patterns were consistent between years (Appendix 1). Additional to territory quality shifts, we also found shifts in foraging patterns. As expected, groups shifted their foraging efforts to the most prey-rich vegetation type as the season progressed. This territory quality change through the breeding season is an important aspect to territory quality assessment and individuals should consider the length of time that territory quality is expected to be high. If a group's territory quality is high enough to begin breeding early in the season, they will potentially have more of a chance to re-nest in the event of a failure. Similarly, if a group resides on a territory with sufficient quality after peak breeding period, they would have increased re-nesting or second-brooding opportunity. Our results showed that ani groups occupying territories with a high percentage of guinea grass in their territory began breeding earlier, again, suggesting that guinea grass is an important contributor to territory quality.

Per capita analyses are necessary for evaluation of individual advantages. By using per capita territory quality and per capita reproductive success we found that small groups have significant breeding advantages over large groups because they share success with fewer members. Previous studies on guira cuckoos (*Guira guira)* and the groove-billed ani (*Crotophaga sulcirostris)* also found that per capita reproductive success linearly decreased with larger group sizes (Macedo, 1992; Koford et al., 1990). However, per capita reproductive success is complicated in this breeding system and may not be a true reflection of individual reproductive success (Koford et al., 1990). Not all females in communal groups contribute equally to the clutch (Vehrencamp, 1977). On-going microsatellite analyses in our lab are determining reproductive skew and examining competitive strategies among group members.

Communal joint-nesting threshold model

The communal joint-nesting threshold model applies to all communally breeding species in which individuals or pairs disperse from their natal territory and have the opportunity to join an existing group. This model first assumes that group members defend territories varying in quality, and that territory quality influences reproductive success. Our study confirmed this latter assumption with a significant correlation between territory quality (per capita) and per capita reproductive success. A third assumption of the model is that there is a cost to individuals when sharing a territory. Egg tossing and egg burial are competitive behaviors exercised in multi-female groups of anis. Competition increases with group size (Schmaltz et al., in prep.) and this is confirmation that there is cost to sharing a territory. Because anis join large roaming groups during the dry season (Quinn and Startek-Foote, 2000) we assume that they are able to assess the quality of local territories, meeting the forth assumption that prospecting individuals can assess territory quality and survey available opportunities. A final assumption states that individuals are free to settle where their expected reproductive success is greatest. Chasing and fighting occurs during some group-joining attempts (Quinn and Startek-Foote, 2000). Although it appears to be a war of attrition, persistent individuals or pairs are able to join groups. The critical prediction tested in this study was that groups on territories with the best breeding situation obtain the most members. Our finding of a significant negative correlation between group size and territory quality (per capita) falsifies the communal joint-nesting threshold hypothesis. From the data presented, we have shown that smaller groups are occupying the highest per capita quality territories and acquiring the highest per capita reproductive success, yet group-living persists in this, and other joint-nesting species.

Advantages of group living

We show in this study that reproductive benefits and territory quality benefits are not among selective forces favoring joint-nesting. Ecological characteristics do not seem to distinguish joint nesters from other cooperative breeders but male incubation does, and may have contributed to the evolution of joint-nesting (Koford et al., 1990; Vehrencamp, 2000). Habitat saturation has also been suggested as a possible evolutionary route, although contradicting results have been found for Crotophagids (Koford et al., 1986; Macedo and Bianchi, 1997; Lentz et al., Chapter 3). We propose four possible group-living advantages: (1) shared incubation, (2) prolonged survival, (3) predator defence, and (4) influences of ecological factors not measured in this study. Shared incubation may lower mortality of breeders. All cooperative joint-female systems have male-biased incubation, with the dominant male performing the nocturnal incubation (Vehrencamp, 2000). Males that do not contribute to nocturnal incubation are freed from this high risk task (Koford et al., 1990). Survival is an important fitness component and may be prolonged for individuals in groups. A study on the joint-nesting groove-billed ani, a close relative to the ani, found females to have higher survival rates in larger units (Vehrencamp et al., 1988). Increased foraging efficiency and protection from predators may increase survival. During foraging, one or several individuals in a group fly to perches on a fence or tree acting as a sentinel, alarming group members when predators approach (G. Schmaltz pers. obser.). Loflin (1983) suggested that having sentinels may be one of the primary advantages for group living in the smooth-billed ani. Woolfenden (1975) and Alvarez (1975) suggested group-living serves as a defence against nest predation and territory invasion. Lower nest predation rates in multi-pair groups has been shown in groove-billed anis (Vehrencamp, 1978). Additionally, different types of costs and benefits to different members of the group may explain this system. Subordinates may benefit from increased protection and gain experience pertaining to reproduction and social living while dominant individuals may gain fitness advantages by fathering a larger proportion of the incubated clutch. With on-going genetic studies we hope to confirm or dismiss these possibilities.

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Table 2.1. Variables measured for each group in the study area. Territory quality was measured using the per capita territory quality calculation.

Group	Year	Group Size	Reproductive Success	Territory Size (m^2)	TQearly	TQpeak	TQlate	TQAvg
4-Way	2003	3	3	45,904	541,775	1,123,095	844,311	836,393
Casablanca	2003	3	4	76,346	940,362	1,594,345	1,270,435	1,268,381
Congrejos	2003	3	2	99,754	1,499,766	2,433,684	2,024,032	1,985,827
Finca Newfie	2003	2	0					
Gully	2003	3	1	63,246	845,342	1,441,908	1,152,888	1,146,713
Hill Top	2003	2	1	34,534	758,158	983,413	880,256	873,942
Home	2003	3	5	156,986	1,943,849	3,444,067	2,712,359	2,700,092
North East	2003	5	2	129,261	956,273	1,883,031	1,505,918	1,448,407
North Farm	2003	5	0	22,529	223,853	308,011	262,635	264,833
North Hillside	2003	3	2	129,223	1,709,362	3,116,658	2,416,270	2,414,097
North House	2003	12	1	219,604	883,659	1,251,605	1,058,062	1,064,442
North West	2003	13	0	170,392	501,229	922,739	720,666	714,878
South Fence	2003	7	0	72,490	361,479	869,417	631,773	620,890
US Flag	2003	3	4	49,369				
4-Way	2004	4	5	92,527	674,262	1,651,234	312,417	879,304
Casablanca	2004	3	0	40,874	393,607	950,097	183,346	509,017
Citgo	2004	6	4	43,357				
Congrejos	2004	5	0	85,561	532,166	1,040,095	292,239	621,500
East Central	2004	2	3	100,609	1,526,480	3,180,561	781,463	1,829,501
East Citgo	2004	4	4	110,173				
Finca Newfie	2004	4	0					
Garbage	2004	7	7	85,642				
Gully	2004	5	2	85,159	465,294	985,703	238,543	563,180
Home	2004	3	3	82,293	626,834	1,547,953	303,167	825,985
North East	2004	7	0	84,176	382,906	741,993	213,930	446,276
North Farm	2004	2	2	109,180	1,713,444	2,823,002	998,473	1,844,973
North House	2004	5	0	55,165	352,779	631,604	198,620	394,334
North West	2004	7	0	134,894	538,743	1,197,511	266,920	667,725
Porton	2004	4	0					
South Airfield	2004	3	0	68,090	687,130	1,421,069	355,065	821,088
South Central LA	2004	9	5	97,313	303,716	768,720	144,725	405,720
South Fence	2004	8	6	107,977	401,964	972,356	189,217	521,179
Termite	2004	9	0	140,183	443,015	987,997	226,554	552,522
US Flag	2004	17	6					

Table 2.2. Spearman rank correlations between initial date of egg incubation and specific variables.

	Date Incubation Begins
Territory Quality	$r = 0.19, n = 22, p = 0.396$
Group Size	$r = -0.15, n = 22, p = 0.432$
Percent buffel grass	$r = -0.01, n = 22, p = 0.960$
Percent guinea grass	$r = -0.53, n = 22, p = 0.010$
Percent hurricane grass	$r = 0.23, n = 22, p = 0.283$
Percent lantana	$r = 0.29, n = 22, p = 0.181$

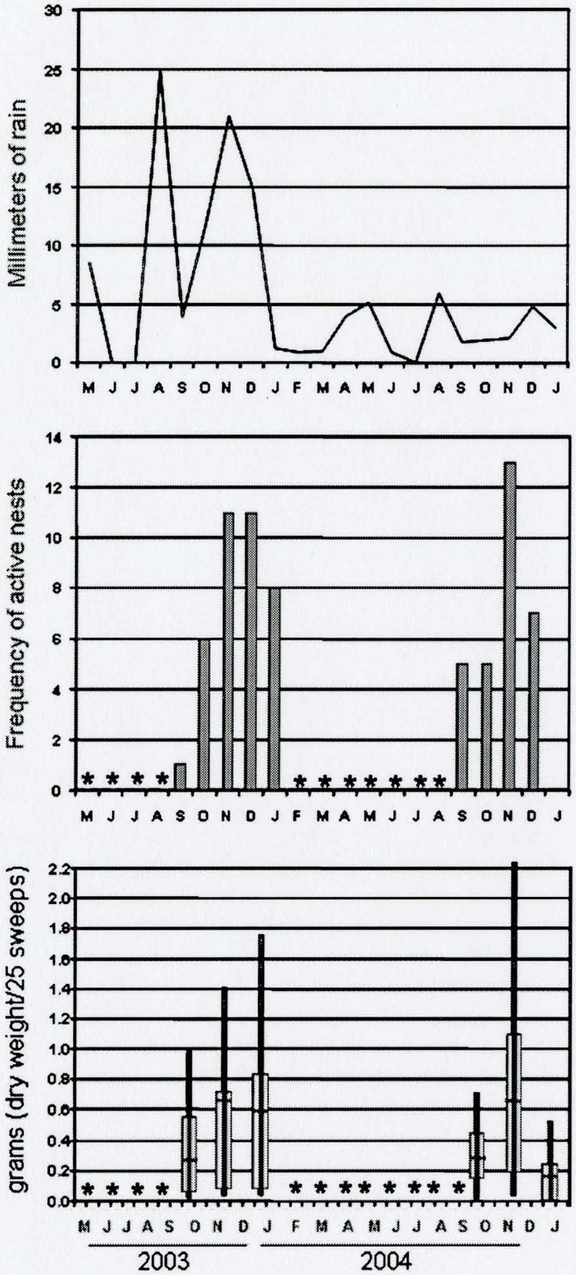

Figure 2.1. Rainfall, the number of active nests, and insect biomass for the major study period (2003 and 2004). Columns with an asterisk indicate that data are not available for these months.

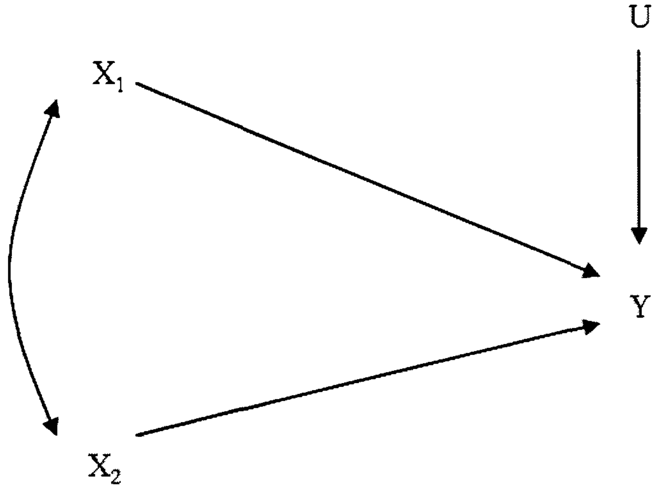

Figure 2.2. Path diagram showing two correlated predictor variables, X_1 and X_2, and an independent variable, U (a composite of all the unknown sources of unexplained variation), affecting one criterion variable, Y.

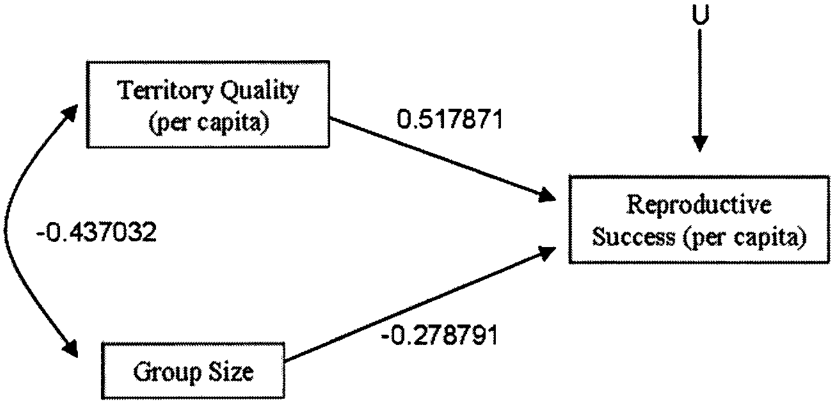

Figure 2.3. Path coefficient diagram showing two correlated predictor variables, territory quality and group size, and an independent variable, U (a composite of all the unknown sources of unexplained variation), affecting reproductive success. Numbers between independent and dependent variables are standardized partial regression coefficients. The double-headed arrow indicates a correlation between the two predictor variables and the number shown between these variables is the Pearson regression coefficient.

Appendix to Chapter 2

Table 1. Spearman rank correlations between per capita territory quality, per capita reproductive success and group size. Although significance changed between years, the direction of the correlation coefficient was consistent.

	2003 ($n = 12$)	2004 (n = 14)
Territory quality$_{(pc)}$ with Reproductive success$_{(pc)}$	$r = 0.73, p = 0.007$	$r = 0.59, p = 0.02$
Territory quality$_{(pc)}$ with Group Size	$r = -0.45, p = 0.13$	$r = -0.68, p = 0.007$
Reproductive success$_{(pc)}$ with Group Size	$r = -0.72, p = 0.007$	$r = -0.40, p = 0.14$

CHAPTER 3

A test of habitat saturation in the plural-breeding smooth-billed ani (*Crotophaga ani*)

ABSTRACT

The habitat saturation hypothesis was developed to explain the evolution of group-living in cooperatively breeding birds. It suggests that offspring remain in their natal territory and delay reproduction because of a local absence of suitable breeding habitat. We investigated the habitat saturation model in the communal joint-nesting smooth-billed ani (*Crotophaga ani).* Anis occur in groups of 2-17 individuals, with multiple breeding pairs per group. Members are usually unrelated but occasionally contain young from previous years. Breeding females in the group contribute to a single clutch of eggs and both sexes cooperate to care for young and to defend the territory. Sites that were not occupied over several years of research (historically unoccupied) and sites that were occupied some years and not others (occasionally occupied) were identified and compared to sites consistently occupied by ani groups using eight ecological variables. Discriminant analysis distinguished between historically unoccupied sites and occupied sites, revealing that a high percentage of guinea grass and a low percentage of hurricane grass may influence occupancy. Our analysis did not discriminate between occasionally occupied sites and occupied sites, indicating that there are available sites for breeding that remain unused in some years. We conclude that the habitat is not saturated. It remains possible that limited breeding opportunities contributed to the evolution of sociality but group-living is not maintained under these conditions. Group-living in Crotphagids is most likely related to intrinsic characteristics of sociality and at least some individuals must benefit from the presence of other group members. *Key words: Crotophaga ani*, joint-nesting plural breeding, habitat saturation.

INTRODUCTION

The evolution of cooperative breeding appears to be based on ecological constraints (Emlen, 1982) that may be classified as high cost of reproduction, shortage of mates, or shortage of breeding sites. Limited breeding habitat, as a constraint driving cooperative breeding, has become known as the habitat saturation model (Selander, 1964; Brown, 1974; Koenig and Pitelka, 1981; Emlen, 1982; Koford et al., 1986; Walters et al., 1988). This model posits that young individuals delay dispersal and remain in their natal unit because of a local absence of suitable habitat for breeding. Upon reaching sexual maturity, these individuals become helpers to the breeding pair on their natal territory and may gain benefits such as indirect fitness, reproductive experience, and territory inheritance (Woolfenden and Fitzpatrick, 1984). A refinement of the model suggests that a severe limitation or absence of marginal habitat, lower quality habitat that would allow reduced reproductive success, would promote dispersal delay and cooperative breeding (Koenig and Pitelka, 1981). In the absence of marginal habitat, young are expected to stay on natal territories as helpers and wait for high-quality vacancies (Zack and Ligon, 1985; Komdeur, 1992).

In the event of a socially restricted setting (i.e. habitat saturation), non-breeding adults have several options. These options include delayed breeding in natal territory, dispersal to an established territory, floating (continuous movement from territory to territory in an attempt to find a vacancy), and mate or nest sharing (Brown, 1983). The habitat saturation model was developed for communal single-breeding (helper-at-the-nest) systems, where offspring do not disperse immediately but, instead, remain as helpers in their natal territory until a breeding opportunity occurs. Plural-breeding, a less common form of cooperative breeding, is characterized by a social unit having more than one breeding female (Koford et al., 1990). Members of these groups are usually unrelated but, occasionally, contain offspring from previous years (Brown, 1978). It is important to know if limited breeding opportunities can also help explain the evolution and maintenance of plural breeding because some plural breeding systems in birds (Acorn Woodpecker, *Melanerpes formicivorus*; Mexican jay, *Aphelocoma ultramarine*) exist under habitat saturation (Koenig and Pitelka, 1981; Stacey, 1979; Brown and Brown, 1984). Macedo and Bianchi (1997) tested the habitat saturation model in the communal joint-nesting guira cuckoo (*Guira guira)* and applied the habitat saturation model to plural breeding systems because some groups retain young, groups may attempt to breed more than once in a season, and because some adults in a group are excluded from breeding.

The smooth-billed ani (*Crotophaga ani)* is a joint-nesting plural-breeding cuckoo of sub-family Crotophaginae. Members of ani groups are usually unrelated, but occasionally contain offspring from previous years. Groups contain anywhere between 2 and 17 adults made up primarily of socially monogamous pairs (Quinn and Startek-Foote, 2000). Breeding females lay their eggs in a single nest. Both sexes cooperate to provide care for the offspring and to defend the territory. Competitive behaviors, including egg tossing and egg burial, have been documented in this species (Quinn and Startek-Foote, 2000). The breeding season begins with the onset of the rainy season when arthropod prey becomes abundant (Quinn and Startek-Foote, 2000).

Previous studies of habitat saturation in other Crotophaginae, led to opposing conclusions. Koford et al. (1986) found that a groove-billed ani (*Crotophaga sulcirostris)* population in Costa Rica lived under conditions of habitat saturation, while Macedo and Bianchi (1997) found evidence against habitat saturation in a population of guira cuckoos (*Guira guira)* in central Brazil. Here we revisit this question with a careful examination of smooth-billed ani territory quality and occupancy in Puerto Rico. The objectives of this study were to (1) determine whether smooth-billed anis live under conditions of habitat saturation, and (2) determine which ecological characteristics distinguish occupied from unoccupied territories. We tested the hypothesis that anis maintain group-living because there is a local absence of suitable breeding habitat. We predicted that unoccupied territories are unsuitable for breeding by anis and we tested this by comparing occupied and unoccupied territories. We further predicted that all suitable habitats are occupied and dispersal options are not available. This critical prediction was tested by analyzing various ecological variables to determine if there are suitable and available breeding habitats.

METHODS

Study area

The research site was located in southwest Puerto Rico at the National Wildlife Refuge (17°59'N, 67°10'W). The study area was approximately 3,300,000 square meters. The habitat was dry, predominated by exotic grasses with scattered trees and was surrounded by populated rural areas and farm fields.

General field methods

We conducted this study from September 2003 to January 2004 and from September 2004 to January 2005; dates that span the rainy season and peak breeding season. We captured anis using mist nets, funnel traps with lure birds, and remote control nest traps (Mock et al., 1999). We measured, took a blood sample from, and color-banded every adult captured. We placed a light-weight transmitter on one healthy individual from each group in most cases. These individuals usually stayed with the rest of the group and during each telemetry session we recorded data including group size, group locations by GPS (Global Positioning System) coordinates, and vegetational foraging type. We performed an average of 8.5 ± 1.05 SE telemetry sessions on each transmitted bird (range 2-15). We transferred GPS coordinates, recorded during telemetry sessions and opportunistic observations, of group activities and locations to ArcView 3.2. We enclosed locations by a straight line to form a polygon defining the total area of utilized territory.

Each year we identified and named groups in the study area according to their location, even though group membership, territory size, territory shape, and relative composition of vegetation types changed between years. To confirm that group membership changed from year to year, we calculated a proportion of shared dyads (Lentz et al., Chapter 2). We found an average shared-dyad proportion of 0.064 ± 0.036 SE for groups in our study area (Range 0 – 0.333), indicating that on average 6% of the individuals in the group remained from one year to the next. Territory size and shape changed from year to year (Figure 3.1). When consistently occupied territories changed shape, unused parts of the habitat previously used were encroached by neighbors and the territory remained occupied. Territories that were used one year and not another remained available in the unused year, as neighbors did not intrude on the unused habitat.

In this study we assumed that during breeding a group's territory and home range were the same. In other words, this species does not have a home range that is larger than its breeding territory. We base this on observations that a group never crossed defended territory boundaries, even when neighboring residents were not present. During the study period we documented the locations of territorial disputes during telemetry sessions (n = 3) and during opportunistic sightings (n = 3). Following disputes, telemetry records (n = 143) and opportunistic sightings showed no group crossing over the established boundary. We also documented instances where two groups were within 25 meters of each other at the presumed territory boundary with no disputing (n = 6) and assumed disputes to settle boundary location were previously carried out. Following these sightings, there was no record (telemetry sessions, opportunistic sightings) of the groups crossing over the inferred boundary when the neighbors were not present. These documented instances suggest that during the breeding season when territories are held, groups do not forage beyond their territorial boundaries, thus we assume that home range is equal to defended territory.

We identified 8 ecological variables that are important to the quality of a territory and measured these variables for 26 different groups (12 groups in 2003, and 14 groups in 2004) and for 5 vacant but seemingly ecologically-similar areas. Observations by our group since 1998 (personal observations by JSQ) and documented territory data, showed no ani groups had resided in these 5 vacant sites during the time research has been taking place in this study location. We circumscribed the five unoccupied sites in ArcView 3.2 and calculated area. The ecological variables measured for unoccupied and occupied sites were (1) percent buffel grass (*Centris ciliaris)*, (2) percent guinea grass (*Panicum maximum)*, (3) percent hurricane grass *(Fimbristylis spathacea)*, (4) percent lantana (*Lantana involucrate)*, (5) percent other (including pavement, bare ground, buildings, and roads), (6) total area of tree canopy, (7) number of available nest trees, and (8) number of available roost trees. During telemetry sessions we identified buffel grass, guinea grass, hurricane grass, and lantana as the most common foraging species in the area for the smooth-billed ani as a total of 94.5% of all recorded foraging minutes were spent in one of these four vegetational species. We determined the total area of predominant vegetation by using an aerial photo as a guide and confirming vegetation type by ground-truthing (Lentz et al., Chapter 2). We determined the area of individual vegetation type for each territory in ArcView 3.2. We calculated total canopy area for each territory in ArcView 3.2 by outlining the area covered by tree canopy using an aerial photo from 1999. We defined available nest sites as an alive Mesquite tree or a Rolon tree greater than 2 meters in height and defined available roost sites as alive trees greater than 2 meters.

We sweep-netted to evaluate prey abundance because anis are insectivorous. Sweep-netting was found to be the most accurate method to represent the types of prey eaten by ground feeding insectivores (Poulin et al., 1992). We measured arthropod abundance, for the four predominant vegetational species, three times during each breeding season. Sampling occurred as follows: October 14-16 (early), Nov 28-29 (peak), and January 4-6 (late) in 2003 and October 9-10, November 20-21, and January 3-4 in 2004. We took a 25-sweep sample with one step of about one meter taken for every vigorous sweep of the net. We identified arthropods to order and then sun-dried them for a total of 24 hours. We calculated biomass (g dry weight/25 sweeps).

Data analysis

We divided telemetry sessions into early, peak and late season and tallied foraging time in each vegetation type during each season. To test if foraging patterns in the late season of 2004 (dry) were different from the rest of the sampling periods (wet), we used a two-way ANOVA with vegetation species and time of season as independent variables and time foraging as the dependent variable. We used a one-way ANOVA to test if the percent foraging time differed for vegetation species during the late season of 2004. We used discriminant analysis to determine whether occupied territories were distinguishable from unoccupied areas using the eight ecological variables listed above Discriminant analyses are used to determine which variables discriminate between two or more naturally occurring groups (Huberty, 1994). Canonical (CAN) variables, linear combinations of the variables that summarize the differences between the two groups, were included in the discriminant analysis. By plotting two of these canonical variables, CAN1 and CAN2, one can visualize how well they discriminate among the groups (Huberty, 1994). Similarly we compared territories that were occupied each year with those occupied only one of the two study years with a discriminant analysis. We used SAS 9.1.2 (SAS Inc.) for all data analyses. All tests are two-tailed with an alpha value of 0.05. Herein descriptive statistics are given as means ± standard error.

RESULTS

Study population and breeding efforts

In this study population, ani breeding group sizes averaged 5.3 (± 0.59, *n* = 34) and ranged from a pair to 17 birds. The average territory size for these groups was 94,116 ± 9,027 square meters (*n* = 26; range 34,534–219,604; Figure 3.1). Many groups had more than one breeding attempt in a season (1.4 ± 0.134; range 0-3). In 2003, three groups successfully raised more than one brood and four groups re-nested after a failure earlier the same season. In 2004, one group successfully raised more than one brood and four groups re-nested after a failure earlier the same season. Groups that had more than one breeding attempt (either re-nested or raised more than one brood) produced an average of 2.42 fledglings per breeding season (± 0.54; *n* = 12), and group with only one breeding attempt produced and average of 2.22 fledglings per breeding season (± 0.49; n = 23); a difference that is not significant (t-test: $t_{34} = -0.255$, $p = 0.80$).

Nests sites, roosts sites and canopy cover

Nests were built mostly in Mesquite or Rolon trees (87%). Nest-tree height averaged 6.76m (± 0.34; $n = 67$) and nest height averaged 5.08 (± 0.29; $n = 67$). The number of Mesquite and Rolon trees in a territory varied from 6 to 106 (Table 3.1) and was positively correlated with territory size (Spearman rank correlation: $r = 0.55$; $n = 26$; $p < 0.01$). The number of Mesquite and Rolon trees in a territory did not correlate with reproductive success (Spearman rank correlation: $r = -0.007$; $n = 26$; $p = 0.971$) nor with per-capita reproductive success (Spearman correlation: $r = -0.08$; $n = 26$; $p = 0.695$).

Predominant vegetation

Percent buffel grass, percent guinea grass, percent hurricane grass, and percent lantana varied among occupied and unoccupied territories (Table 3.1). Prey availability for all vegetational types sampled was highest during the peak sampling period (Table 3.2). Foraging patterns were not significantly different between the dry and wet season. (Two-way ANOVA, season: $F_{1,20} = 0.271$; $p = 0.612$, vegetational type: $F_{3,20} = 1.838$; $p = 0.194$, season * vegetational type: $F_{3,20} = 1.328$; $p = 0.311$). Foraging efforts were highest in guinea grass during the early (53% of a total 1907 foraging minutes) and peak

(45% of a total 1414 foraging minutes) breeding season. Foraging efforts during the late breeding season in 2004, a representation of a dry period, were highest in hurricane grass (One-way ANOVA: $F_{3,16} = 6.531$; $p = 0.004$; Figure 3.2). Percent time foraging in hurricane grass was significantly higher than percent time in every other vegetation type (Tukey post hoc; Appendix 1).

Occupied and unoccupied territories

We observed several areas that were consistently unoccupied by groups of smooth-billed anis and other areas that were occupied some years and not others. Consistently occupied and historically unoccupied sites (sites that were not occupied over several years of research by our group) were significantly distinct from each other (Discriminant analysis: $F = 3.89$; $p = 0.0059$). Analysis indicated that percent guinea grass and percent hurricane grass were the main variables contributing to the first canonical variable, and hurricane grass and buffel grass were the main variables contributing to the second canonical variable (Figure 3.3). Unoccupied sites had a significantly higher percentage of guinea grass (Kruskal-Wallis: $p < 0.01$) and a significantly lower percentage of hurricane grass (Kruskal-Wallis: $p < 0.01$). We noted four territories that were occupied one year and vacant the next. Three of the four territories were reproductively successful (at least one young fledged from the nest).

Occasionally-occupied sites and occupied sites were not distinguishable using discriminant analysis (*F* = 0.85; *p* = 0.574; Figure 3.3).

DISCUSSION

Territories differ in prey availability, number of nesting and roosting sites, tree density, and other ecological variables, all of which may be important to the fitness of a group. For our study we considered ecological characteristics that could affect survival and reproduction. The amount of prey varies for different area of dominant plant coverage throughout a season (Table 3.2) and adequate food availability is important for survival and successful rearing of young (Lemon, 1991; Jetz et al., 2003). It may also be important for a territory to contain several available nest sites. Anis do not reuse nests (Quinn and Startek-Foote, 2000) but may re-nest in the same tree. If a clutch is taken by a predator, an additional nest site will be required. Canopy cover is also important for survival as it provides protection from aerial predators.

One objective of this study was to determine which ecological characteristics distinguish between occupied and unoccupied territories. Of the eight ecological variables measured, percentage of guinea grass and percentage of hurricane grass were the only two ecological variables to distinguish between these groups. Percent guinea grass in a territory may play a role in determining when a group begins reproductive activity (Lentz et al., Chapter 2). Guinea grass produced the highest arthropod abundance during the peak season of 2003, and second highest during the peak season of 2004 (Table 3.2). All unoccupied territories showed above-average percentages of guinea grass. This indicates that groups could reside and breed in these territories during the peak season, as prey abundance would be more than adequate. Hurricane grass appears to be an important species during dry periods (Figure 3.2).

Above average amounts of rain fell late in the 2003 breeding season and prey abundance better represented a peak season (Table 3.2). The breeding season in 2004 was consistent with average amounts of rain for the region (1980-2004 rain data provided by US Fish and Wildlife). The late part of breeding season in 2004 became dry and there was a significant decline of arthropod abundance, as expected. During this dry time hurricane grass had the highest arthropod abundance (Table 3.2) and foraging efforts were shifted to this species (Figure 3.2). The unoccupied territories show a range of 0 - 1.27% hurricane grass and this could be a critical determinant in territory choice.

We did not examine all characteristics of a territory. Densities of rats and feral cats, ani predators, may have varied throughout the study area. However, we did not notice any patterns indicating increased predator densities on territories of small groups.

We noted four territories that were occupied one of the two study years and vacant the other. Statistically there were no differences between these sites and sites regularly occupied. Three of these four territories were reproductively successful indicating they were, in fact, territories suitable for nesting. We did not find the habitat of our population of smooth-billed anis to be saturated. Some sites were never occupied because there are territory characteristics that presumably limit breeding. In contrast with expectations of habitat saturation there were suitable sites available for breeding that were not in used in some years. Thus, we reject the hypothesis that anis maintain group-living because of a local absence of suitable breeding habitat.

There are notable shortcomings with previous tests of the habitat saturation hypothesis using guira cuckoos and groove-billed anis. Koford et al. (1986) provided a detailed analysis on how reproductive success is influenced by various ecological factors. The authors calculated the probability of successful dispersal and tested if the habitat existed under conditions of saturation. They obtained the probability of successful dispersal by comparing the number of potential new breeders to the number of breeding opportunities created by mortality. The authors concluded that costs of dispersal were relatively low and that the habitat was saturated, based on findings of excess production (Koford et al., 1986) We suspect that adult mortality could not accurately be measured, as it is not possible to distinguish between mortality and dispersal of adults unless dead anis are found or banded individuals are seen in an area outside the study site. Even if accurate measures of adult mortality were obtained, habitat saturation is best supported by strong evidence that there are no unoccupied territories that are suitable for breeding. Koenig and Pitelka (1981) and Emlen (1982), when developing an extension to the habitat saturation model, hypothesized that habitat saturation will occur when all suitable habitats are filled and continuously occupied and unoccupied territories are rare. Excess production may imply a saturated habitat, but does not support that all suitable habitats are occupied.

More thorough support for the habitat saturation hypothesis comes from removal experiments where constraints are relaxed (Hatchwell and Komdeur, 2000). One such experiment transferred Seychelles warblers (*Acrocephalus sechellensis)* to an unoccupied island to test if habitat saturation played a role in the evolution of cooperative breeding. When the warblers were first transferred there was no cooperative breeding but as high-quality sites were filled, young birds began to stay as helpers (Komdeur 1992). Similar results have been reported for red-cockaded woodpeckers, *Picoides borealis* (Walters et al., 1992) and superb fairy wrens, *Malurus cyaneus* (Pruett-Jones and Lewis, 1990).

Removal experiments are not always feasible. Alternatively one may show habitat saturation by documenting that all suitable habitats are occupied. Macedo and Bianchi (1997) compared sites occupied by guira cuckoo groups with vacant sites using 14 ecological variables. They found that there were no significant differences between occupied and empty sites concluding that the habitat is not saturated because it contained suitable vacant sites. Evidence of sites occupied one year and vacant the next confirmed this result. Despite this appropriate method for testing the habitat saturation hypothesis, Macedo and Bianchi (1997) made some important assumptions that were not examined critically. First, they assumed that the nest site was at the center of group's territory and that the area centered on the nest tree (50m radius) represented the vegeatational characteristics of the entire territory. Our Figure 3.1 clearly shows that this is not the case for the smooth-billed ani. Second, they assumed that all territories were the same size, which is not the case in our study (Figure 3.1). Macedo and Bianchi (1997) found no differences between occupied and empty sites and concluded that the habitat was saturated. However, they did not actually measure territory boundaries and empty sites could have been occupied. There also could have been unused areas that were assumed to be occupied (because they were within 100m of nest). These areas may have been ecologically different than occupied areas.

We used a methodology similar to Macedo and Bianchi's (1997) with some improvements. We found that there are suitable habitats available for reproduction, yet group-living persists in the smooth-billed ani. We conclude that group-living in Crotphagids is most likely related to intrinsic characteristics of sociality and that at least some individuals in a group benefit from the presence of other group members. These group living advantages may include, (1) shared incubation, (2) prolonged survival and (3) predator defence (Vehrencamp, 1978; Lentz et al., Chapter 2). These social benefits are consistent with the relatively unusual trait of male incubation in cooperative joint-female systems (Vehrencamp, 2000). Incubation is costly and if dominant males perform nocturnal incubation, subordinate members are freed from this high-risk task. These social benefits and perhaps even asymmetrical benefits (benefits that vary qualitatively among group members) may maintain group living. We do exclude the possibility the habitat saturation was involved in the evolution of sociality but suggest that social benefits are most likely maintaining group-living in the smooth-billed ani.

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Table 3.1. Ecological variables measured for occupied (minimum, maximum and averages shown) and unoccupied territories.

	OCCUPIED			UNOCCUPIED				
	Minimum	Maximum	Average	UO1	UO2	UO3	UO4	UO5*
Territory Size (m^2)	34,534	219,604	93,093	85,391	68,265	54,371	33,575	14,778
Territory size (per cap) (m^2)	4,505	54,590	21,715	-	-	-	-	-
Number of individuals that could reside	-	-	-	4	3	2-3	2	1
Percent buffel grass	0	79.64	18.46	8.35	6.7	0.89	0.3	65.22
Percent guinea grass	4.06	89.36	41.81	87.68	89.68	92.13	99.7	32.99
Percent hurricane grass	0	86.92	32.03	0	1.27	0.22	0	1.18
Percent lantana	0	11.45	2.03	3.35	2.42	6.27	0	0
Percent other	0	19.24	5.4	0.63	0.32	0.38	0	0
Area Canopy (m^2)	1,476	70,989	27,407	31,145	24,922	6,586	8,961	1,769
Available Nest trees	6	106	46	77	33	34	58	5
Available Roost trees	6	110	49	77	33	34	66	5

* Excluded from analyses because territory size was not large enough to contain even one breeding pair

Table 3.2. Average dry weight ± standard error in grams of arthropods per 25 sweeps, based on 27 samples, for the 4 vegetational types during three sampling times.

	Buffel grass		Guinea grass		Hurricane grass		Lantana	
	2003	2004	2003	2004	2003	2004	2003	2004
Early Sampling	0.48 ± 0.11	0.35 ± 0.06	0.33 ± 0.11	0.27 ± 0.06	0.58 ± 0.15	0.34 ± 0.10	0.21 ± 0.06	0.14 ± 0.03
Peak Sampling	0.54 ± 0.14	0.78 ± 0.12	0.87 ± 0.34	0.74 ± 0.11	0.69 ± 0.25	0.54 ± 0.09	0.62 ± 0.25	0.46 ± 0.12
Late Sampling	0.48 ± 0.07	0.16 ± 0.03	0.62 ± 0.14	0.12 ± 0.04	0.62 ± 0.10	0.20 ± 0.02	0.50 ± 0.11	0.16 ± 0.04

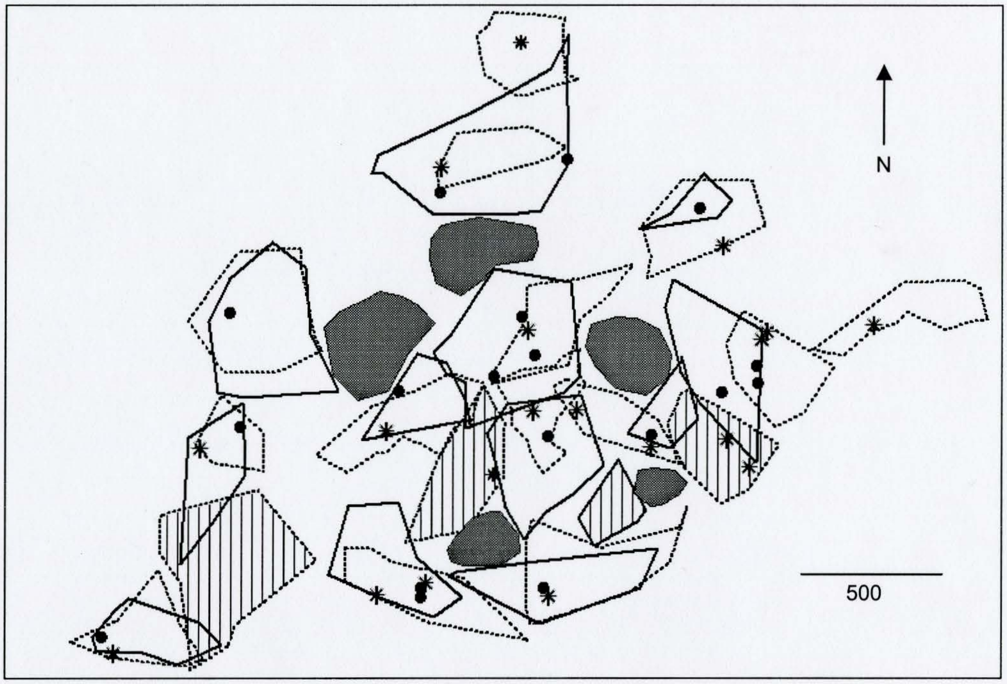

Figure 3.1. Map of study area showing historically unoccupied areas (shaded), single-year-occupied territories (lined), and area that were occupied both years (clear) with the 2003 year boundary (solid line) and 2004 (dashed line) boundaries indicated. 2003 nest sites are identified as a solid dot and 2004 nest sites are identified as a star.

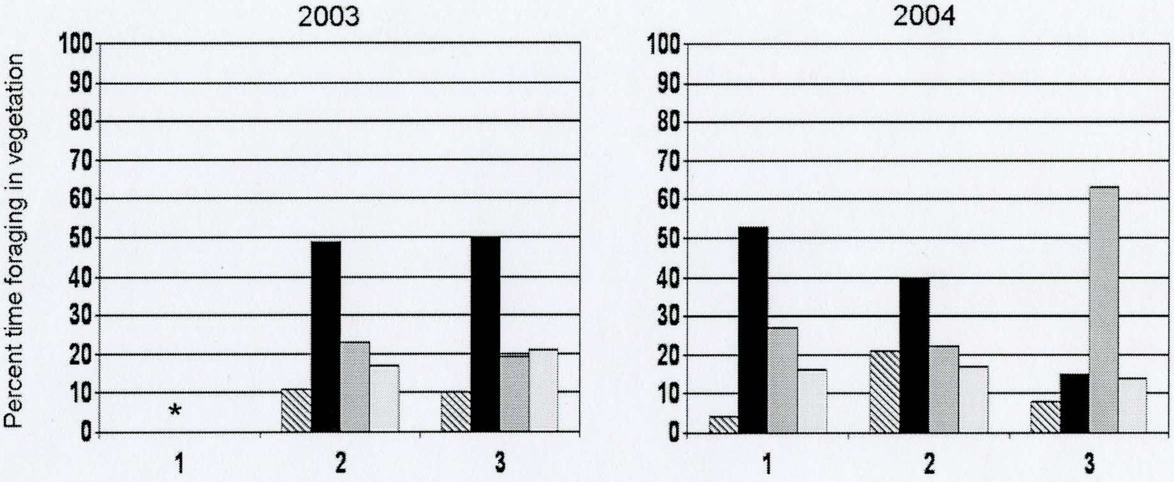

Figure 3.2. Histograms of percent time spent foraging in the predominant vegetation types: buffel grass (diagonal lines), guinea grass (black), hurricane grass (grey), lantana (white) during the early season (1), peak season (2) and late season (3) in 2003 and 2004. Column with an asterisk indicates that foraging data were not collected during this time.

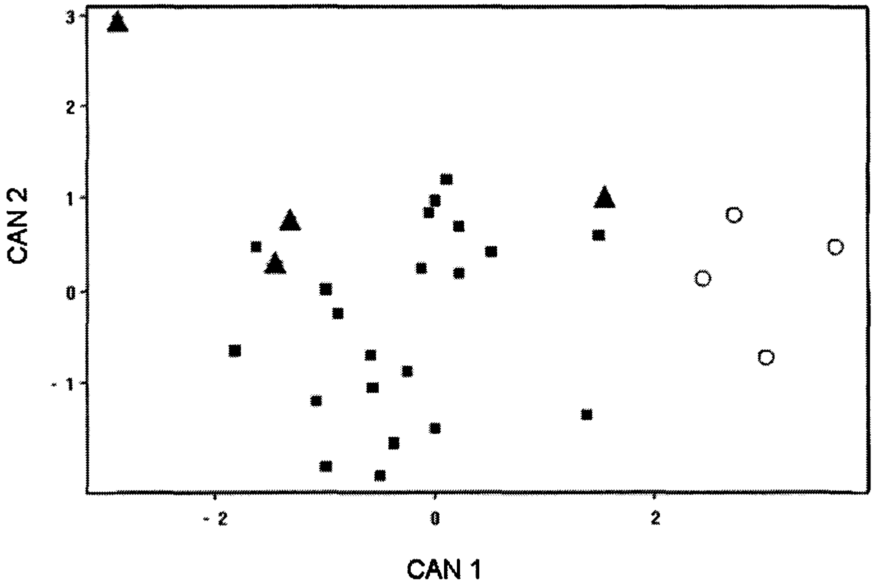

Figure 3.3. Plot of canonical variables CAN 1 and CAN 2 output from the discriminant analysis. Open circles are unoccupied sites, triangles are sites occupied one year but not another, and squares are sites occupied both years.

Appendix to Chapter 3

Table 1. Summary of Tukey post hoc results for the one-way ANOVA test of the effect of vegetation type on percent foraging time.

				95% Confidence Interval	
(I) Vegetation	(J) Vegetation	Mean difference** (I-J)	Significance	Lower Bound	Upper Bound
Buffel	Guinea	-7.40000	0.973	-56.8976	42.0976
	Hurricane	-67.10000*	0.007	-116.5976	-17.6024
	Lantana	-7.50000	0.972	-56.9976	41.9976
Guinea	Buffel	7.40000	0.973	-42.0976	56.8976
	Hurricane	-59.70000*	0.016	-109.1976	-10.2024
	Lantana	-0.10000	1.000	-49.5976	49.3976
Hurricane	Buffel	67.10000*	0.007	17.6024	116.5976
	Guinea	59.70000*	0.016	10.2024	109.1976
	Lantana	59.60000*	0.016	10.1024	109.0976
Lantana	Buffel	7.50000	0.972	-41.9976	56.9976
	Guinea	0.10000	1.000	-49.3976	49.5976
	Hurricane	-59.60000*	0.016	-109.0976	-10.1024

* The mean difference is significant at the 0.05 level

** Standard error of the mean difference is 17.3; SE (diff) = SQRT (2*MSwithin) / n)

CHAPTER 4

General conclusion and future directions

GENERAL CONCLUSION

The purpose of this thesis was to find an accurate measure of territory quality and to relate it to communal breeding and fitness of group members. I tested the communal joint-nesting threshold hypothesis to determine if individuals live in groups because they are compensated with a high-quality territory. I also tested the habitat saturation hypothesis to determine if this ecological constraint possibly contributed to the evolution of joint-nesting plural-breeding mating systems. Results from both chapters two and three led to similar conclusions. Chapter two revealed that there are per capita territory quality and per capita reproductive benefits to being in a small group. Chapter three revealed that there are suitable breeding habitats available for small groups. However, despite reproductive advantages for small group and available habitats for small groups, group-living persists. These two chapters concluded that there are not obvious group-living benefits and that one must consider other explanations for the evolution and maintenance of this system.

All cooperative joint-female systems have strong male incubation (Vehrencamp, 2000). Incubation is costly, especially during the night when an individual is the sole protector of the nest and itself against nocturnal predators. We have unpublished video evidence suggesting that more than one individual in a group performs nocturnal incubation. In a group setting, some subordinate members may be freed from this high-risk position. This shared incubation may lower mortality of breeders and is a possible group-living benefit (Koford et al., 1990). Survival may be prolonged for individuals in groups for other reasons as well. During foraging, anis engage in sentinel behaviour where one or several individuals in a group perch on fences or trees, acting as a lookout and alarming group members when predators approach. Anis are insectivorous and forage in short to medium-length grass (Quinn and Startek-Foote, 2000). Group members usually forage near each other, although not always within sight of each other, explaining why sentinel behaviour is so important and how it may prolong life. A study on the joint-nesting groove-billed ani found females to have higher survival rates in larger units (Vehrencamp et al., 1988). Loflin (1983) suggested that having sentinels might be one of the primary advantages for group living in the smooth-billed ani.

Defence against nest predation and territory invasion is another possible group-living advantage (Woolfenden, 1975; Alvarez, 1975). In most tropical birds, nest predation is very high (Ricklefs, 1969). During my study time in Puerto Rico, I observed nest predation by fire ants (*Solenopsis invicta)*, red tail hawks (*Buteo jamaicensis)*, feral cats (*Felis domesticus)*, and rats (*Rattus rattus*) as well as by an unidentified species. The eggs predated by the unidentified species looked like a bird had pecked at them. Groups are able to defend their nests and territories better than a single pair. A lower predation rate on nests in multi-pair groups has been shown in groove-billed anis (Vehrencamp, 1978).

In addition to social and longevity advantages, there are costs and benefits to different members within each group. Subordinate males that do not contribute to nocturnal incubation may gain by avoiding this high risk task. Subordinates may also gain protection from group members and experience pertaining to reproduction and social living. Dominant males in a group may gain a fitness advantage of fathering a larger proportion of the incubated clutch (currently under investigation by our group). Female breeding roles may also be hierarchical as Koford et al. (1990) distinguished breeding roles in female groove-billed anis on the basis of egg laying order. Results showed that the last laying female was favoured with the greatest number of eggs in the incubated clutch. In a study on groove-billed anis, Vehrencamp (1977) showed that in two-female nests, the second female to lay owned 63% of the incubated clutch and in three-female nests, the division was (1^{st} 24%, 2^{nd} 30%, 3^{rd}, 46%). Additional evidence showed that ownership of eggs in the incubated acorn woodpecker clutch favoured the egg-removing female (Mumme et al., 1983). Genetic studies are the only way to determinate exact contributions to incubated clutches, and to understand exact costs and benefits of different members within a group.

From the studies I have presented here I show that there are not obvious group-living benefits and that there must be other explanations for the evolution and maintenance of this system. Below are listed some directions for future research that I feel will advance our knowledge in group-living benefits, maintenance of this social system, and behavioural strategies in joint-nesters.

1. Year Effects: One question that arose during the course of this study was whether the results I obtained were due to year effects. This study was conducted during the breeding season of 2003 and 2004. According to rainfall data provided by US Fish and Wildlife, 2004 received an average amount of rain for the region, but 2003 received two and a half times the average amount. Despite different climate conditions between the 2003 and 2004 breeding seasons, similar qualitative patterns between group size, reproductive success, and territory quality were found (Appendix 1 to Chapter 2). During an especially dry breeding season, patterns may be different. Preliminary analyses (using data from 1998-2004) suggested that group size did not change between years (One-way ANOVA: $F_{6,116} = 0.07, p = 0.706$), but observations (Pers. Comm. G. Schmaltz) and data from our group's long-term research suggested that larger groups may gain reproductive advantages during the dry years. Statistical analyses have not yet determined if this is the case. Additional data on both wet and dry breeding seasons are needed to identify if large groups have reproductive advantages in dry breeding seasons. Territory quality data should also be collected during a dry breeding season to identify if patterns are still consistent between years.

2. Comparison of study sites: In Puerto Rico there are three study areas of which we have access: Cabo Rojo, Laguna Cartegena, and Uplands. Although these sites are within several kilometres of each other, habitat and rain patterns are very different. Vehrencamp (1978) faced similar conditions in Costa Rica where her study area was pastureland and agricultural fields with small pockets of marsh. The western third of the area was entirely marsh. An in-depth study showed significant differences between groups residing in marsh areas and groups residing in pasture areas. Adult mortality was lower in marsh habitat. Female reproductive rate was higher in the marsh area, but male reproductive rate was higher in the pasture. Larger groups in the pasture habitat were more successful at preventing nest predation than pairs, but there was no effect of group size on predation in the marsh. Food levels were approximately the same in both habitats (Vehrencamp, 1978). A territory quality, group size, reproductive success, and prey availability comparison between Cabo Rojo, Laguna Cartegena (more lush than CR), and Uplands (drier than CR) would add valuable knowledge to how habitat affects various group living parameters.

3. Insect sampling. Early in the development of this project, one objective was to determine if anis match reproductive efforts with the highest peaks of prey availability in their specific territory. Because insect samples were taken only three times during the breeding season (Chapter 2), it was difficult to answer this exact question. All territories had highest territory quality during the peak sampling period (Table 2.1). In this study we attained some reproductive timing answers, but to test if timing of reproduction matches exact peaks of prey availability, vegetation should be sampled more frequently throughout the breeding season. To maximize efficiency of arthropod sampling, I suggest that future researchers conduct sweep-net sampling at fewer locations (Appendix 1). If time is still limited, I would suggest sampling only guinea grass (important species during the wet periods) and hurricane grass (important species during the dry periods).

4. Genetic confirmation: In a complex breeding system, such as the smooth-billed anis, genetic data are essential in answering specific questions. On-going microsatellite analyses in our lab (Blanchard and Quinn; Gregory and Quinn, *In Press*) are currently determining reproductive skew and examining competitive strategies among group members. In this study we assumed equal reproductive success among same-sex individuals. With the help of genetic data, we would be to confirm the number of breeding adults in a group to obtain accurate per capita values. We have determined that group-living benefits are an important aspect to this breeding system. Genetic analyses will be able to determine advantages received by various members within group.

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Appendix to Chapter 4

Table 1. GPS coordinates of sweep-net sampling locations. Locations with an asterisk are easily accessible and I suggest future researchers continue to conduct sweep-net sampling at these locations.

NAME	LATITUTE	LONGITUDE
ABG1*	1989255.00	693044.00
ABG2	1989290.00	693098.00
ABG3	1989037.00	692997.00
AGG1*	1989065.00	693090.00
AGG2	1989085.00	692635.00
AGG3	1989092.00	693319.00
AHG1*	1989807.00	693316.00
AHG2	1989514.00	692902.00
AHG3	1989067.00	692630.00
ALB1	1989224.00	692998.00
ALB2*	1989284.00	693094.00
ALB3	1989787.00	693426.00
BBG1	1989959.00	693623.00
BBG2*	1989373.00	693997.00
BBG3	1989391.00	693632.00
BGG1*	1989093.00	693727.00
BGG2	1989243.00	694071.00
BGG3	1989869.00	693969.00
BHG1*	1989688.00	694034.00
BHG2	1989420.00	693965.00
BHG3	1989956.00	693627.00
BLB1*	1989883.00	693900.00
BLB2	1989304.00	694075.00
BLB3	1989396.00	693626.00
CBG1	1990156.00	694325.00
CBG2*	1989260.00	694306.00
CBG3	1989161.00	694474.00
CGG1*	1989172.00	694237.00
CGG2	1990171.00	694341.00
CGG3	1989998.00	695051.00
CHG1*	1989933.00	694103.00
CHG2	1990155.00	694344.00
CHG3	1990087.00	694535.00
CLB1	1989161.00	694244.00
CLB2*	1989973.00	695077.00
CLB3	1989282.00	694281.00
DBG1	1988737.00	693554.00
DBG2*	1989057.00	693478.00
DBG3	1988969.00	693005.00
DGG1	1988646.00	692934.00
DGG2*	1989060.00	693462.00
DGG3	1989047.00	693283.00
DHG1*	1988150.00	693083.00
DHG2	1988244.00	693261.00
DHG3	1988569.00	693327.00
DLB1	1989021.00	693192.00
DLB2	1988837.00	692960.00
DLB3*	1988184.00	693086.00
EBG1*	1988902.00	693820.00
EBG2	1989128.00	693843.00
EBG3	1988817.00	694007.00
EGG1*	1988945.00	694097.00
EGG2	1988904.00	693830.00
EGG3	1989007.00	693624.00
EHG1	1988842.00	694080.00
EHG2*	1988900.00	693761.00
EHG3	1988692.00	693864.00
ELB1	1989022.00	693745.00
ELB2	1988735.00	693619.00
ELB3*	1989028.00	693643.00

NAME	LATITUTE	LONGITUDE
FBG 1	1988571.00	694525.00
FBG 2 *	1988780.00	694803.00
FBG 3	1988754.00	694164.00
FGG1	1988875.00	694117.00
FGG2	1988684.00	694318.00
FGG3*	1988943.00	694710.00
FHG1	1989126.00	694531.00
FHG2 *	1988944.00	694716.00
FHG3	1988991.00	694405.00
FLB1*	1989149.00	694507.00
FLB2	1988968.00	694110.00
FLB3	1989022.00	694672.00
GBG1	1988027.00	692783.00
GBG2 *	1988104.00	693270.00
GBG3	1988130.00	693077.00
GGG1	1988047.00	692754.00
GGG2 *	1988185.00	692887.00
GGG3	1987780.00	692703.00
GHG1 *	1988089.00	693347.00
GHG2	1988159.00	692934.00
GHG3	1988148.00	693126.00
GLB1 *	1988307.00	693280.00
GLB2	1988198.00	692976.00
GLB3	1988183.00	692896.00
HBG1	1988015.00	693750.00
HBG2 *	1988089.00	694206.00
HBG3	1988653.00	694295.00
HGG1 *	1987982.00	693883.00
HGG2	1988453.00	693310.00
HGG3	1988686.00	693850.00

NAME	LATITUTE	LONGITUDE
HHG1	1988440.00	693297.00
HHG2*	1988563.00	694269.00
HHG3	1988696.00	694201.00
HLB1	1988033.00	693721.00
HLB2*	1988397.00	694248.00
HLB3	1988503.00	693890.00
IBG 1	1988494.00	694413.00
IBG2	1988101.00	694222.00
IBG3*	1988229.00	694502.00
IGG1	1988545.00	694311.00
IGG2	1988457.00	694520.00
IGG3 *	1988102.00	694369.00
IHG1 *	1988344.00	694663.00
IHG2	1988121.00	694548.00
IHG3	1988423.00	694394.00
ILB1	1988389.00	694269.00
ILB2	1988226.00	694268.00
ILB3 *	1988472.00	694305.00