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Reviewed work(s):

Source: *Journal of Avian Biology*, Vol. 28, No. 3 (Sep., 1997), pp. 207-215

Published by: [Wiley](#) on behalf of [Nordic Society Oikos](#)

Stable URL: <http://www.jstor.org/stable/3676971>

Accessed: 15/02/2013 14:11

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Communal breeding in tropical Guira Cuckoos *Guira guira*: sociality in the absence of a saturated habitat

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Macedo, R. H. and Bianchi, C. A. 1997. Communal breeding in tropical Guira Cuckoos *Guira guira*: sociality in the absence of a saturated habitat. – J. Avian Biol. 28: 207–215.

The evolution of sociality in many communally breeding birds has been ascribed to a lack of optimum habitat, that is, insufficient high quality resources to allow dispersal and independent breeding of young. In these species, offspring do not disperse immediately, but instead remain as helpers in their natal territory until a breeding opportunity occurs. We examined the habitat saturation model for a communally breeding South American species, the Guira Cuckoo. This species breeds in large groups composed of both related and unrelated individuals. Nestlings also exhibit varying degrees of relatedness, or they may be completely unrelated. Thirteen ecological variables were measured in 14 sites occupied by groups and compared with data from nine vacant sites that appeared similar. Data concerning breeding traits were collected for each reproductive event. Guira Cuckoos exhibit tactics that reduce the reproductive success of others within the group, mainly egg-tossing behavior and, occasionally, infanticide. Potential nesting sites within territories, in the form of araucaria trees, varied greatly in number, but there was no relation between their availability and the size of the group controlling the area. Group size was significantly positively correlated with grass cover within territories, but unrelated to the other 12 vegetation variables measured. Empty sites had a significantly greater abundance of prey items than did areas occupied by Guira Cuckoos, which may indicate depletion of insects due to the cuckoos' foraging activities. No other significant differences were found between occupied and empty sites. These results suggest that habitat saturation may not be an important factor in the maintenance of group-living in Guira Cuckoos. However, this does not exclude the possibility that habitat quality may have an important effect on reproduction. The basis for group-living in this species is most likely related to intrinsic characteristics of sociality that increase survival and lifetime reproductive fitness.

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Several species are characterized by communal breeding systems, in which group members contribute care to young that are not their offspring. Individuals remain in their natal units and may delay reproduction for one or several years (Brown 1978). In these social systems, a single breeding pair per unit is the norm (denominated communal singular-breeding, Brown 1978), and the helpers are usually older siblings of the nestlings. On the other hand, in communal plural-breeding systems (Brown 1978), a social unit has more than one breeding female, and non-breeding helpers may or may not occur. Plural breeding is far less common and has

been documented for only a handful of species. Among those fairly well studied are: the Acorn Woodpecker *Melanerpes formicivorus* (Koenig 1981, Koenig and Mumme 1987), the Mexican Jay *Aphelocoma ultramarina* (Brown and Brown 1990), the Pukeko *Porphyrio porphyrio* (Craig 1979, Craig and Jamieson 1990), the Groove-billed Ani *Crotophaga sulcirostris* (Vehrencamp 1978, Vehrencamp et al. 1988), the Smooth-billed Ani *C. ani* (Loflin 1983) and the Guira Cuckoo *Guira guira* (Mariño 1989, Macedo 1992, 1994).

Explanations in the literature usually relate the phenomenon of communal breeding to ecological factors

(Brown and Balda 1977, Gowaty 1981, Koenig 1981, Koford et al. 1986). Alexander (1974) and Koenig (1981) stress that there are three general classes of elements that select for group-living: (1) predator defense; (2) food-supply exploitation patterns; and (3) location of a limited resource, such as quality habitat and/or mates. This last category, specifically as related to habitat, has taken the form of a very popular hypothesis to account for the evolution of cooperative breeding, that of ecological saturation of the habitat, first proposed by Selander (1964). It has, since then, received the support of many authors (Brown 1974, 1987, Stacey 1979, Koenig and Pitelka 1981, Emlen 1982, Woolfenden and Fitzpatrick 1984, Koford et al. 1986, Koenig and Mumme 1987). According to this model, which was developed with communal singular- (but not plural) breeding in mind, young birds, physiologically capable of reproducing, remain in the territory where they were born because there is a local absence of habitat suitable for breeding. It therefore becomes adaptive, for both parents and adult offspring, for the latter to remain in the natal unit and help rear younger siblings until a breeding vacancy becomes available (Woolfenden and Fitzpatrick 1984).

The habitat saturation hypothesis has been little tested, in spite of its persuasive appeal, and recently has been questioned for several species where it appears that other factors, in addition to habitat saturation, have been important in shaping current breeding systems (Wiley and Rabenold 1984, Zack and Ligon 1985, Stacey and Ligon 1987, Ford et al. 1988).

Stacey and Ligon (1991) proposed an alternative hypothesis to explain communal breeding, which emphasizes the benefits accrued by young helpers remaining in their natal territories, rather than the breeding restrictions resulting from ecological constraints. In their "benefits-of-philopatry hypothesis," Stacey and Ligon (1991) suggest that it should be advantageous for young birds to remain in their natal units if one or both of the following are true: (1) when the local territories vary greatly in quality; and/or (2) group-living, per se, is important for survival and/or reproduction, thus leading to an optimal group size for a given area. If one or both criteria are not met for a given species, that is, there is no among-territory variance and/or there are no survival/reproductive advantages associated with group-living, an individual should always disperse whether or not the habitat is saturated.

In this study, our objectives were to: (1) analyze whether habitat saturation is an important factor influencing the maintenance of group-living in the South American Guira Cuckoo, a communal plural breeder with joint nesting; and (2) determine whether certain vegetational characteristics affect breeding parameters of groups.

The breeding system of the Guira Cuckoo study-population, located in central Brazil, is detailed in Macedo

(1992). Briefly, these birds build a joint nest, with as many as 13 adults engaged in each breeding effort, and with several females laying eggs. Both males and females incubate the eggs and help care for nestlings. There is considerable reproductive conflict within groups, as evidenced by egg ejection and infanticidal behavior (Macedo and Bianchi 1997, Melo and Macedo, unpublished data). DNA-fingerprinting analyses (Quinn et al. 1994) revealed that: (1) nestmates are the offspring of different adults in the group; (2) some adults are excluded from breeding; and (3) polyandry and polygyny may occur within any given group. As outlined above, both cooperative as well as competitive tactics exist within groups. In such a scenario, one would expect group members to disperse to unoccupied and suitable territories whenever possible, especially if such individuals have been excluded from breeding. In previous studies of this species (Macedo 1992, 1994), a puzzling aspect has always been the presence of what appeared to be suitable habitat, but which remained vacant throughout the breeding season. Here we present data that address this issue: the non-dispersal of group members and the maintenance of group-living, despite obvious disadvantages, in an unsaturated habitat of homogeneous quality. We evaluate the habitat saturation hypothesis by comparing ecological attributes of occupied sites with other empty but apparently suitable areas.

Methods

The research site is located on the Brazilian central plateau (elevation 1158 m), in the suburban area of Brasilia (15°47'S, 47°56'W). The habitat in the study area is a mosaic of savanna grassland, dense native shrubs and trees, interspersed with cultivated areas and residential gardens. Guira Cuckoos nest predominantly in araucaria trees *Araucaria angustifolia*, a species native of southern Brazil and introduced in the area, which provides a measure of protection because of its prickly leaves and trunk. Guira Cuckoos actively defend their territories, some of which contain several araucaria trees exhibiting vestiges of old nests. In undisturbed areas, Guira Cuckoos usually choose other prickly vegetation as nesting sites. In southern Brazil, Guira Cuckoos also nest in the native araucaria trees (M. Andrade, pers. comm.). Breeding and ecological data were collected from August 1994 to March 1995, which coincides with the rainy season and peak breeding activities of the Guira Cuckoo. Reproductive variables recorded were: (1) group size; (2) eggs laid; (3) eggs tossed; (4) eggs hatched; and (5) fledglings.

Ecological attributes were measured in 14 sites occupied by groups and compared with data from 9 vacant but ecologically similar and adjacent areas. The unoc-

cupied sites were selected randomly from a subset of areas regularly searched because they contained araucaria trees and appeared similar in vegetational characteristics to occupied territories.

The methodology used for describing habitat was somewhat similar to that of Bednarz and Ligon (1988) in their study of the Harris' Hawk *Parabuteo unicinctus*, with some modifications to suit the objectives of our study. Previous data indicate that Guira Cuckoos usually forage and remain within 300 m of their nests (although territory size was not measured in this study). In occupied as well as unoccupied sites, a circle with a radius of 50 m was centered on the nesting tree (or an araucaria tree in vacant areas). Vegetation within these circles was assumed to be representative of the rest of the territory. Within this circle, all trees and shrubs (over 1 m) had the following measured: (1) estimated height; and (2) two perpendicular diameters of the canopy. The same measures were taken for all araucaria trees within a plot of 100-m radius. Shrub and tree densities were determined by the direct count of all individuals within the 50-m radius. For araucaria trees, the height of the lowest branch was measured to allow subsequent estimate of the tree's vertical density. Two perpendicular 100-m line transects were centered on the nest tree (the directions of which were decided at random). Along these lines, the percent cover of savanna, ornamental grass, litter, bare or paved ground was estimated using the line-intercept method (Mueller-Dombois and Ellenberg 1974).

Guira Cuckoos are largely insectivorous (small vertebrates are consumed occasionally). Prey abundance was estimated by standard sweep-net sampling. At each site, four 100-pace samples were taken, with each sample centered on the nest tree (or araucaria tree in empty site) and extending out in perpendicular directions from each other. All sampling took place within three months of the rainy season, and was conducted before noon. The insects and spiders sampled were killed with ethyl acetate and dried overnight in an oven and their dry weight was taken as an estimate of biomass.

The variables used in the analyses were: (1) % savanna = mean percentage of native grassland; (2) % grass = mean percentage of ornamental grass; (3) % ground = mean percentage of bare or paved ground; (4) % litter = mean percentage of litter cover; (5) % canopy = percentage of circle area covered by tree and shrub canopy; (6) woody plants = the number of shrubs (> 1 m high) and trees within the area of the 50-m radius circle; (7) vegetation height = mean height of all shrubs (> 1 m high) and trees within the area of the 50-m radius circle; (8) araucarias = the number of araucaria trees within a radius of 100 m of the nesting tree (in vacant areas an araucaria was randomly selected as the plot's central point); (9) araucaria height = mean height of araucaria trees within a radius of 100 m; (10) araucaria importance = density \times mean height of arau-

caria trees; (11) araucaria compactness = availability of dense araucaria trees (average araucaria height – average height of first branch); (12) prey abundance = number of insects and spiders from net-sweep samples; (13) prey biomass = dry weight of net-sweep samples.

To detect differences between occupied and non-occupied sites, univariate analyses of the variable estimates were conducted using a one-way Kruskal–Wallis test. Discriminant analysis was used to determine whether territories could be distinguished from empty areas with respect to the habitat variables measured. Our hypothesis was that several variables would possibly be good predictors of occupation by Guira Cuckoo groups. In this analysis, proportional variables (% savanna, % grass, % ground, % litter and % canopy) were arcsine transformed.

Frequently, group size, reproductive success, and other reproductive parameters are related to particular characteristics of a species' habitat. Since Guira Cuckoos exhibit a marked preference for nesting in the prickly araucaria trees, we explored the possibility that the number of these trees available within a group's territory might be associated with average or maximum group size. In several instances in the past, more than one araucaria has been occupied simultaneously by a reproducing group and, usually, sequential nesting attempts occur in different trees within the territory. For this evaluation we counted all araucaria trees within 100 m of the nest and, using group-size data from 1987 to March 1995 (when available for a territory), attempted to correlate maximum and average group sizes with number of araucaria trees available. We also explored the association between other ecological variables and group size. Additionally, we examined the possibility that group size might affect the number of breeding attempts in a season (one versus two), or average reproductive success of group members. We used Pearson correlation to explore the possibility that vegetational characteristics might be associated with the total number of surviving fledglings produced in each territory during the study.

Results

The potential nesting sites and their occupancy pattern are shown in Fig. 1, for four breeding seasons (1987, 1988, 1990 and 1994). In four territories, Guira Cuckoos bred more than once in the 1994/95 season (Table 1). Of the three for which group sizes could be ascertained, two increased in size in their second attempt, whereas one retained its initial size. However, group size does not determine whether or not the group will attempt to breed twice in a given rainy season. The average number of individuals in groups of known size that bred only once (\bar{x} = 5.14, SE = 1.01, N = 7) was

Table 1. Breeding parameters of Guira Cuckoo social units during the 1994–1995 season.

Territory	Group size	Eggs			Chicks		Breeding attempts
		laid	tossed	hatched	disappeared	fledged	
D2	5	6	0	5	4	1	
	9	8	2	5	2	3	2/2
B3	?	4	4	0	—	—	1/0
B2	6	?	?	?	?	2	
	?	16	11	?	?	0	2/1
A2	3	9	9	0	—	—	1/0
B8	3	10	2	5	2	3	
	6	8	1	6	6	0	2/1
C15	3	?	?	6	3	3	1/1
A7	4	5	1	4	2	2	1/1
C10	10	9	0	7	2	5	1/1
A8	?	17	9	8	8	0	1/0
E5	3	9	2	3	3	0	1/0
C13	4	7	7	0	—	—	
	4	10	?	?	?	4	2/1
D4	7	8	0	7	7	0	1/0
C14	6	7	0	6	2	4	1/1

not significantly different from the average number in groups that bred twice ($\bar{x} = 5.80$, $SE = 0.92$, $N = 4$; two-tailed Student's *t*-test, $t = 0.459$, $P = 0.66$). The four groups that bred twice were successful in at least one attempt. Of the groups that bred only once ($N = 9$), five were unsuccessful. Groups breeding twice produced an average of 3.25 nestlings per breeding attempt ($SE = 0.48$, $N = 4$), whereas groups breeding once produced an average of 1.56 chicks ($SE = 0.67$, $N = 9$). The difference is not significant (two-tailed Student's *t*-test, $t = 1.58$, $P = 0.14$). There was no correlation, in this study, between group size and the average reproductive success of adults in the unit.

At almost all nests Guira Cuckoo group members exercised egg-tossing. In only four of the 14 reproductive events discovered during early egg-laying were no eggs tossed. In some instances, such as in territories B3, A2, and C13, the entire clutch was ejected, resulting in the abandonment of the nest. In other cases, large portions of the clutch were evicted: for the second breeding attempt of group B2, 11 of the 16 eggs laid were tossed; for group A8, of the 17 eggs laid, 9 were tossed. If eggs survived the tossing period and hatched, chicks were exposed to considerable mortality as well. In all cases where eggs hatched, at least some of the chicks disappeared from the nest. In seven nests, only part of the brood disappeared, while in four cases, all of the brood was lost. These disappearances occurred sequentially and usually within the first week post-hatch. For group A8, a total of eight chicks were present in the nest on 23 Nov 1994. On 25 Nov, five of the chicks had vanished. On 28 Nov, one of the remaining three chicks had disappeared and two were found dead on the ground beneath the tree. Similarly, for group D4, seven chicks hatched and were present on 17 Feb 1995. Five days later they had all disappeared. Many of these occurrences can be attributed to acts of

infanticide by group members (Macedo and Bianchi 1997, Melo and Macedo, unpublished data).

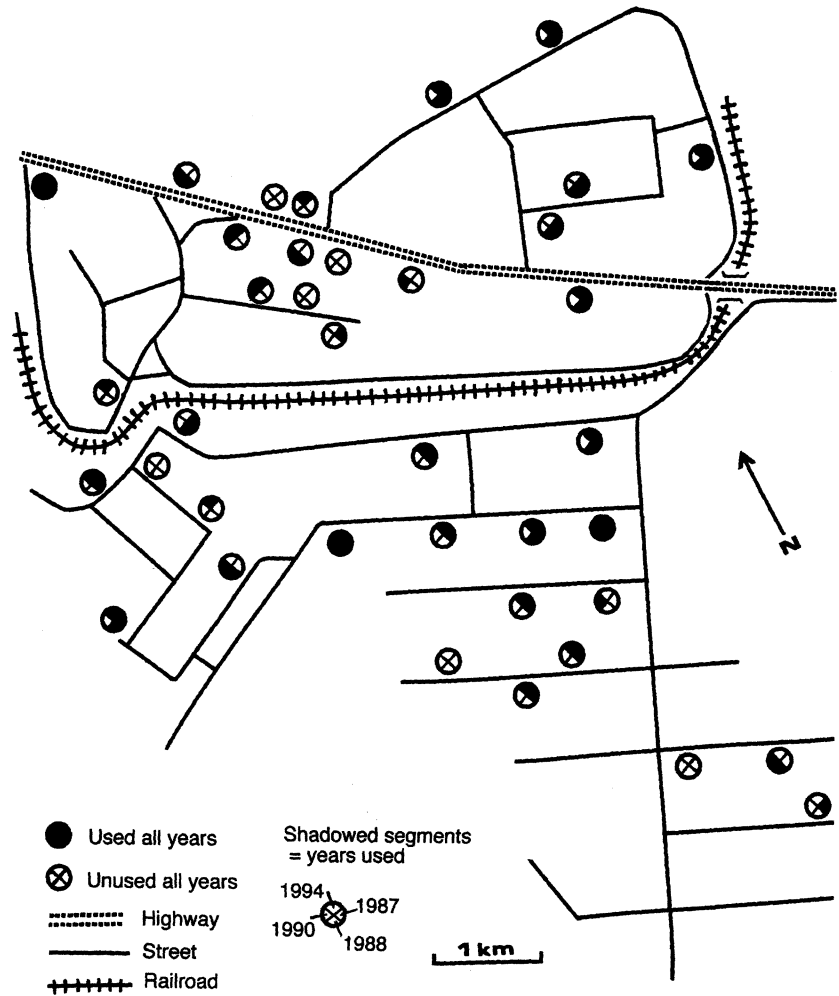
Large differences existed in terms of number of potential nesting sites within territories (Table 2). The number of araucaria trees, which represent ideal nesting sites, varied from only one, as in territory A2, to 31 in territory C13. Group sizes within these territories varied widely as well. There was no linear relationship between group size (mean and largest group sizes: data from 1987 to 1995) and number of araucaria trees available (for largest group sizes: $r = -0.38$, $P = 0.22$; for average group sizes: $r = -0.28$, $P = 0.63$). In some instances large groups, such as the one with nine individuals recorded in territory D2 in 1995, had only two araucaria trees available. In contrast, some areas with dense araucaria stands, such as C13 with 31 trees, were occupied by relatively small groups. In fact, group size varied considerably within a territory in different years: territory B8 ranged from three to 12 individuals, who controlled an area containing three araucarias; territory E5, containing two araucarias, was occupied in different years by three and 10 group members.

In analyzing the association between group size and vegetation variables, we used the largest group size that occupied a territory during the present study. Of all habitat variables, only percent of grass cover was associated with group size ($r = 0.67$, $P < 0.05$).

We also considered whether vegetational characteristics were associated with offspring production in each territory (Tables 1 and 3). Of the habitat variables used in this analysis – percent canopy, savanna, ground, litter and grass cover, woody plants and vegetation height, prey biomass, and araucaria compactness – only prey biomass was significantly correlated with the number of fledglings produced ($r = -0.63$, $P < 0.05$).

The multivariate discriminant analysis did not distinguish occupied from empty sites ($F_{12,10} = 1.171$, $P =$

Fig. 1. Map of study area (Brasilia, Brazil) showing the spatial distribution of Guira Cuckoo nesting sites (circles) during the 1987, 1988, 1990 and 1994 breeding seasons.



0.41). The univariate analysis indicated that, with one exception (prey abundance, Table 3), there were no significant differences between areas occupied by Guira Cuckoo groups and uninhabited areas, for the 13 habitat variables measured. For most variables, the means were very similar. Contrary to what might have been expected, a priori, the values of several vegetational variables were greater, though not significantly so, in sites unoccupied by Guira Cuckoos. For example, the percentage cover of savanna and canopy, woody plants, average araucaria height, importance and compactness, and prey biomass and abundance (the latter significantly so), all had greater mean values in empty areas. Habitat characteristics with greater values in occupied areas included grass, ground and litter cover. The significant difference found for prey abundance is due to an extremely high value that occurred in one of the empty sites (1032 items). Prey abundance values for non-occupied sites, excluding this single site, ranged from 87 to 333 items ($\bar{x} = 200.13$, $SE = 30.63$, $N = 8$). For occupied areas, the number of items collected

ranged from none to 202 ($\bar{x} = 102.43$, $SE = 18.38$, $N = 14$). If we exclude the deviating site, the difference becomes non-significant (Mann-Whitney $U = 31$, $P = 0.09$). It is probable that the high peak of insect abundance at that single location was a random event that may have resulted from local conditions at the time, such as a recent rainfall or nearby fire that herded insects in one direction.

Discussion

In this paper we investigated the habitat saturation model to determine: (1) whether the sites occupied by Guira Cuckoo groups actually differ qualitatively and quantitatively from unoccupied areas; and (2) whether habitat variables of occupied sites affect breeding parameters. Although the habitat-saturation model was developed for communal singular-breeding species, where only one pair reproduces, several factors common to both singular and plural breeding systems indi-

Table 2. Relationship between Guira Cuckoo group size in various years and araucaria availability within the territory. Some territories were vacant during certain phases of the research.

Territory	Araucarias available	Group size (year)	Mean	Range
D2	2	5 (1994)/9 (1995)	7.0	5–9
B2	6	7 (1987)/4 (1990)/6 (1994)	5.7	4–7
A2	1	5 (1987)/3 (1994)	4.0	3–5
B8	3	6, 12 (1990)/3 (1994)/6 (1995)	6.8	3–12
C15	2	3 (1994)	–	–
A7	2	6 (1990)/4 (1994)	5.0	4–6
C10	11	8 (1988)/5, 5 (1990)/10 (1995)	7.0	5–10
A8	19	4 (1995)	–	–
E5	2	10 (1990)/3 (1994)	6.5	3–10
C13	31	4 (1994)/4 (1995)	4.0	4
D4	9	2 (1988)/7 (1995)	4.5	2–7
C14	9	6 (1994)	–	–

cate that the model could be applicable to both. Evidence (Macedo 1992) indicates that in the Guira Cuckoo groups, some young are retained within their natal units for at least one breeding season, and possibly more. During the extended breeding season (from August to March), a group may attempt breeding two or three times. Although groups are usually not composed of related adults, apparently for some time they include adult offspring. Additionally, some adults in the groups are excluded from breeding (Quinn et al. 1994). In this they are similar to singular-breeding species: independent young and/or sexually mature adults could presumably disperse if adequate habitat were available. For these reasons, we felt that the application of the habitat saturation model was justifiable. The second objective of our study relates to habitat quality and its effect upon the reproductive success of individuals in a group. If habitat is not saturated, but habitat variables are associated with such breeding parameters as, for example, group size or reproductive success, the availability of high quality habitat could affect dispersal decisions. In the case of the Guira Cuckoo, the question of why sociality is maintained is especially relevant, given the several negative reproductive consequences of group living for some individuals in the unit.

Previous research shows that Guira Cuckoo breeding units exhibit numerous asymmetries in the degrees of relatedness among adults and nestlings (Quinn et al. 1994). Numerous adults contribute to the parentage of nestlings, and the elevated number of reproductive females yields a high degree of complexity in behavioral interactions, as compared to the smaller breeding units (typically two females) of Groove-billed Anis studied by Vehrencamp et al. (1988). These adult interactions dictate highly competitive behaviors that reduce the fitness of some group members. Egg-tossing is one competitive tactic employed by group members. It is unknown whether both male and female Guira Cuckoos engage in egg-tossing, or whether it is restricted to females. At any rate, the egg-tossing at some nests (e.g. B3, A2 and C13) occurred at such high intensity that the group

abandoned its reproductive effort. In most nests, at least part of the clutch was destroyed in this manner. Furthermore, for those chicks that survive the egg-tossing phase, an added obstacle to fledging remains. In all nests monitored, the sequential disappearance of at least a few chicks occurred. Previous studies, as well as ongoing research, indicate that infanticide may occur regularly, as a form of brood reduction. The circumstantial evidence for infanticide (Macedo and Bianchi 1997), and direct observation of this phenomenon suggest that, although predation, disease and other debilitating factors may be sources of mortality for Guira Cuckoo chicks, infanticide is most likely the prevalent factor behind chick death.

Given these rather dire circumstances associated with group breeding in Guira Cuckoos, the dispersal of group members to suitable and unoccupied breeding sites would appear to be an attractive option. We therefore expected to find that areas occupied by groups would be subtly different from vacant areas. Specifically, unoccupied sites should have different values for several of the resources measured. Additionally, sites occupied by larger groups should have higher resource values for some of the variables, if one assumes that more individuals are capable of defending areas containing more prey, several nesting sites, and more potential hiding places from predators.

In our research on the Guira Cuckoo breeding system, we have registered over the years an occupation pattern that is contrary to the predictions of the habitat saturation model (see Fig. 1). Sites occupied one year may be vacant the next. The fact that they have been occupied is evidence of their suitability, since the main features of the habitat do not change yearly. In fact, throughout a breeding season, sites may remain empty for an extended period, with large communal groups in the neighborhood. Empty and occupied sites are mostly side by side and, typically, present very similar characteristics in terms of vegetation, disturbance levels and water availability during the dry season, when lawns are irrigated.

Table 3. Comparison of habitat variables from areas occupied by groups of breeding Guira Cuckoos and unoccupied areas.

Habitat variables	Occupied sites (N = 14)			Unoccupied sites (N = 9)		
	Mean	SE	Median	Mean	SE	Median
% savanna	10.64	13.88	3.55	27.56	29.55	11.95
% grass	48.83	34.14	54.76	41.23	30.28	42.42
% ground	37.76	21.09	38.49	30.09	24.00	22.62
% litter	6.49	8.69	0.00	1.13	2.83	0.00
% canopy	32.08	18.74	27.87	41.79	17.79	39.98
woody plants	106.86	62.86	91.50	122.00	39.41	120.00
vegetation height (m)	5.19	1.55	4.64	5.33	1.17	5.38
araucaria density	7.36	8.45	3.00	7.33	14.20	3.00
araucaria height	8.94	2.03	9.08	10.54	2.71	10.36
araucaria importance	55.17	54.15	31.86	74.96	121.40	26.01
araucaria compactness	5.53	1.77	5.72	7.18	2.55	6.47
prey abundance*	102.43	68.77	91.00	292.56	288.89	211.00
prey biomass (g)	0.85	1.05	0.36	1.30	1.35	0.66

* $P < 0.01$; Kruskal–Wallis one-way analysis of variance.

With one exception, no significant differences were found between occupied and empty sites. This exception, prey abundance, had a higher value for sites unoccupied by Guira Cuckoos. Although the significance of the test relied on the single outlier with an exceptionally high value, it is possible that the efficient foraging by Guira Cuckoos diminishes the abundance of insects in the territories they occupy. None of the remaining 12 habitat variables were associated with occupancy by groups. In fact, empty territories are not of poor quality but are similar to ones occupied in the neighborhood. Araucaria trees, the nest-site most commonly used, vary widely in number within different territories, but the number of such trees present neither affected occupancy nor size of groups. Larger groups were no more likely than small groups to attempt to breed more than once in a season. For Guira Cuckoos, increasing group size may augment the adverse effects associated with communal breeding. As the number of potentially reproductive females increases, so do egg-tossing and probably also infanticide.

Many investigators have found correlations between group size and vegetation parameters (e.g. Brown and Balda 1977, Gaston 1978, Vehrencamp 1978, Craig 1979, Brown et al. 1983, Zack and Ligon 1985), and the role of habitat in promoting sociality has been widely recognized. For Guira Cuckoos, we considered that vegetational characteristics that could increase survival were: canopy cover (as a means to evade predation from aerial predators); araucaria tree vertical density (to decrease nest detection from below and above); tree and shrub density (providing perches and cover); and the extent of grass (providing optimum foraging substrate). Group size was significantly positively correlated only with grass cover. Guira Cuckoos are ground foragers, preying on insects and small invertebrates in the grass. It is likely that grass provides year-round availability of insects, especially in irrigated lawns. There was no association between group size and the

remaining habitat characteristics. Of the possible habitat variables affecting offspring production, only insect biomass showed a significant and negative correlation. Therefore, both area of grass and insect availability appear to be important elements of Guira Cuckoo territories. However, as mentioned above, both of these habitat parameters had high values also in areas unoccupied by groups.

The evidence presented here suggests that not only does the habitat appear to be unsaturated, but empty sites are almost certainly of high quality. We cannot exclude the possibility, however, that there is some characteristic of the habitat that is extremely important, and variable among years, that we were unable to identify. At any rate, the available evidence indicates that for Guira Cuckoos group-living may have an intrinsic value that offsets the disadvantages mentioned previously. This appears to be the case in several species for which researchers have questioned the appropriateness of the habitat saturation model and suggested alternative explanations.

Rabenold (1984) reported that in the communally-breeding Striped-backed Wren *Campylorhynchus nuchalis*, adult offspring remain in their groups despite the availability of vacated territories. In a study of the ecological factors that determine communal breeding in the Harris' Hawk, Bednarz and Ligon (1988) concluded that extended parental care and cooperative hunting are factors that probably outweigh its costs, and support for the habitat saturation model was weak. Similarly, Zack and Ligon (1985) suggested that *Lanius* shrikes are faced with a "dispersal dilemma," in which an individual has to opt between dispersing to territories with a low perennial shrub cover (and lowered chance of successful reproduction) and natal-territorial fidelity, with the probability of eventually attaining breeding status. For Acorn Woodpeckers the evidence available also does not support the habitat saturation model. Stacey and Ligon (1987) found that, over a 10-year

period, most territories in central New Mexico were not continuously occupied, remaining available for independent breeding to individuals acting as helpers in their natal units. Suitable habitat is therefore not saturated, but cooperative behavior remains common. In Acorn Woodpeckers, high-quality territories which have mast storage trees, are continuously occupied, while lower-quality sites are frequently vacant, although the latter would permit immediate breeding (Stacey and Ligon 1987). Thus, it appears that individuals must evaluate lifetime payoffs associated with either dispersing to breed in low-quality habitat, or remaining in the high-quality area of their natal unit. Research conducted by Komdeur (1992) on the Seychelles Warbler *Acrocephalus sechellensis* included an experimental manipulation of transferring birds to unoccupied areas, thus providing a test of the habitat saturation model. Komdeur (1992) found that birds that were born in high-quality sites, as opposed to those born in medium- and low-quality sites, delayed breeding more often and did not disperse immediately to breed in lower-quality sites. Thus, territory quality is an important factor shaping this species' breeding system.

Our study does not support the habitat saturation model, nor the refinements later suggested by Koenig and Pitelka (1981) and Emlen (1982), according to which high-quality territories are continuously occupied (with few vacancies for dispersing birds) and little marginal habitat is available. These later additions to the model are in accordance with the results of some field studies, as pointed out above. By contrast, our results for the Guira Cuckoo population studied support the "benefits-of-philopatry" hypothesis (Stacey and Ligon 1991) that emphasizes the advantages of group-living and the existence of an optimal group size, rather than constraints imposed by the habitat. The possibility that an optimal group size is important to Guira Cuckoos is similar to what was proposed by Vehrencamp (1978) to explain certain aspects of plural breeding. Thus, if aggregation is advantageous to individuals, they should form units even when adequate habitat is available for independent breeding. In fact, the retention of young may facilitate the achievement of an optimal group size, even if temporarily.

We suggest that sociality in the Guira Cuckoo is associated with benefits other than those of an ecological nature. In some species of birds, territory quality is an essential component of the "benefits-of-philopatry" model. For example, in Acorn Woodpeckers (Koenig and Stacey 1990) the number of storage holes for nuts is a strong component of territorial quality. A bird born on a territory with a high number of storage holes might be better off if it were to remain and delay breeding, because of the access to such an important resource. For the Guira Cuckoos, habitat quality is not the most critical factor determining reproductive success, and there are plenty of high-quality breeding sites

available. Apparently, group cooperation is important enough to compensate for the negative effects of sociality.

There are several behaviors we have observed, though not measured quantitatively, that could be important in this regard. First, groups forage together, usually in a fan-like formation. This may facilitate predator detection and so increase individual survival, while also enhancing foraging capacity by increasing individual foraging time (Powell 1974) and flushing out prey more effectively. We have frequently observed foraging groups that maintain a single individual "on guard," usually on an elevated perch. This guarding system is also in effect around active nests and was monitored for two breeding seasons (Macedo 1994). There is almost continuous surveillance over the nest. Group members threaten potential predators (cats and humans were observed), and have an alarm call that results in the convergence of the group. Other benefits may be important as well: sharing of nest-building, incubation duties and feeding of nestlings.

Thus, while habitat saturation may have served as the propulsive force that shaped communal breeding in several species, it is unquestionable that, for many other species, there are advantages to sociality unrelated to any type of ecological constraint. In the case of the Guira Cuckoos, groups are composed of both related and unrelated individuals, which results in cooperative behaviors as well as less amicable interactions with detrimental reproductive consequences. However, above and beyond positive interactions based on familial bonds, there appear to be advantages gained by group living that contribute to the maintenance of sociality in the Guira Cuckoo.

Acknowledgments – This study was supported by the Fundação de Apoio a Pesquisa do Distrito Federal. We thank Miguel Marini, Paulo Oliveira and an anonymous reviewer for their critical evaluation of previous drafts of this paper. Guarino Colli made helpful contributions to the data analyses. For their help with collecting data during different stages of the field work, we thank Juliana Almeida, Leandro Baumgarten, Helio Cunha, Itamar Dias, Iriane Piva and Daniela Sanckiewicz.

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(Received 31 May 1996, revised 2 December 1996, accepted 19 December 1996.)