ECOLOGICAL FACTORS AFFECTING GROUP AND TERRITORY SIZE IN WHITE-THROATED MAGPIE-JAYS

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Abstract.—White-throated Magpie-Jays (*Calocitta formosa*) breed cooperatively and defend permanent, all-purpose group territories. We measured territory area, resource levels, resource dispersion, group size, and group reproductive success for 14 groups over a three-year period in Costa Rica. Larger groups possessed larger territories containing more bullhorn acacia trees (*Acacia cornigera* and *A. collinsii*), which provided a critical food resource during the dry season. On a per capita basis, however, the number of acacia trees and territory area were the same for group members regardless of group size, and survivorship did not vary significantly with group size. Variation in reproductive success among groups was influenced by two factors: (1) larger groups produced more successful nests per year, and (2) territories with a higher density of acacia trees fledged more offspring per successful nest. Magpie-jays bred in pasture and foraged primarily in woodland; both habitat types were patchily distributed. The dispersion of woodland and pasture patches in the landscape appeared to constrain where jays could form territories, whereas the amount of acacia and other food resources determined the size that groups could attain. We conclude that ecological factors are critical to understanding the White-throated Magpie-Jay social system, along with other social and demographic constraints typically found in avian cooperative breeders. *Received 4 February 1997, accepted 20 August 1997.*

Group territoriality is uncommon in birds and typically is associated with species that breed cooperatively. For most cooperative-breeding species that defend all-purpose territories (i.e. territories used for breeding and feeding; Schoener 1968, Brown 1969), it appears that a shortage of habitat of suitable quality has prevented nonbreeders from establishing territories of their own. These nonbreeders choose to be philopatric and help their parents breed and thereby gain various immediate and deferred benefits (Emlen 1991, Koenig et al. 1992). In most species of birds that defend all-purpose territories, juveniles disperse before the next breeding event, probably because they compete with their parents for breeding resources and food (Brown 1969, Brown and Orians 1970, Johnson and Gaines 1990, Koenig et al. 1992). These dispersers often are forced to live in marginal habitats as inconspicuous subordinates or as nonbreeders in flocks while awaiting a territory vacancy (e.g. Smith 1978, Carmen 1988, Smith and Arcese 1989). Why can the territories of cooperative breeders support more individuals than a pair and their most recent offspring? And given that auxiliaries usually are competent and motivated to breed when territory vacancies become available (Pruett-Jones and Lewis 1990, Komdeur 1992), why are the same numbers of individuals not distributed in smaller groups on smaller territories, resulting in a higher density of territories (and breeders) for the same density of birds?

These questions are difficult to answer because a full accounting of the factors affecting group and territory size must include any active benefits of grouping (including kin-related benefits), costs that result from forming groups (such as resource depletion), the dispersion and density of resources in the landscape, population-wide demographic pressures, variance in territory-holding ability among competing individuals, and the economics of territorial defense in competition with other groups (Bradbury and Vehrencamp 1976, Parker and Knowlton 1980, Brown 1982, Pulliam and Caraco 1984, Waser 1988, Koenig et al. 1992). We measured the variation among territories in ecological characteristics, group size, foraging rates, and group reproductive success for a population of the White-throated Magpie-Jay (*Calocitta formosa*), a cooperative-breeding species in which group sizes are relatively large and all-

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purpose territories are maintained continuously. In this paper, we analyze the relationships among these variables to infer the probable ecological constraints on territory size in this species.

White-throated Magpie-Jays live in territorial social groups that typically consist of five to six adults; a substantial number of solitary floaters also occur in the same population (Innes and Johnston 1996, Langen 1996a, b). Magpie-jays have a highly unusual social system: (1) territorial groups consist primarily of related, matrilocal females; and (2) males disperse from their natal territory by two years of age to exist as floaters or join another territorial group (Langen 1996b). One pair is responsible for most of a group's breeding attempts, but other group members assist with nest defense and feeding the breeding female and her offspring (Skutch 1953, Innes and Johnston 1996, Langen 1996b). Group members associate while foraging and give a variety of visual and auditory signals that alert others to the presence of food, predators, and conspecific intruders (Langen 1996c). Territories are defended year-round, and boundary disputes involve all nearby group members.

STUDY AREA AND METHODS

Study site and population.—The study was conducted at the administrative center of Santa Rosa National Park, Guanacaste Conservation Area, Guanacaste Province, Costa Rica (10°50'N, 85°37'W) from April 1991 to August 1993. We followed 14 groups that inhabited adjacent territories. The vegetation at the study site was a heterogeneous matrix of recently burned or mowed pasture, old pasture overgrown with woody vegetation, young second-growth woodland, and more mature second-growth dry forest. Different vegetation types had a patchy distribution that resulted from past human activities (primarily cattle ranching that included annual burning) and recent land-use changes associated with establishment of a national park (Janzen 1986).

Although primarily flat, the landscape includes steep canyons and low hills. The dry season at Santa Rosa (December to May) is characterized by strong desiccating winds, high ambient temperature, leafless trees, and few insects. The rainy season (May to November) is cooler, plants grow leaves, and there is a flush of caterpillars and other insects (Janzen 1986, 1993).

We marked more than 200 jays with colored plastic leg bands. Adults were captured and banded throughout the study period, and nestlings were banded at about 10 days posthatching. Unbanded birds (maximum of two per group) were identified by unique plumage patterns (Langen 1996b). At least twice a month, the identity of all individuals seen during focal foraging samples (see below) was recorded. In addition, a census was performed before breeding commenced (January to February), during the middle of the breeding season (May to June), and after all offspring had fledged (August to September). Groups were monitored repeatedly during the breeding season (February through July) for reproductive activity (see Langen 1996a, b). Group size was calculated as the number of birds more than one year of age that were permanent residents within a territory (hence, excluding floaters). We defined group reproductive success as the number of young fledged from all nests within a territory during a breeding season. We also distinguished two components of group reproductive success: (1) the number of fledglings per successful nest, and (2) the number of successful nests per breeding season.

Territory area, habitat composition and resources.—Members of each of the 14 groups were followed by an observer for a cumulative minimum of 50 h over 10 days to map territory use. Members of most of the groups also were followed during regular focal foraging samples (see below). We mapped every group member we encountered during these focal samples and during all other monitoring of the 14 groups that occurred in the three years of the study. Territory boundaries were inferred from daily ranging patterns and frequent disputes with adjacent groups. Territories usually overlapped by less than 50 m.

The area, habitat composition, and quantity of important resources were measured in seven territories during June to August 1992 and the remaining seven territories during June to August 1993. All 14 territories were occupied continuously from 1991 to 1993, and data on group size and group reproductive success were collected during each of the three years. A 50 × 50 m grid was set up and extended to the boundaries of each territory. At each grid point, the habitat type was classified as woodland (closed canopy of woody plants), pasture (grassland with scattered woody plants only), or park (mowed areas around inhabited buildings and campsites). The area covered by each habitat type (in ha) was then estimated by multiplying the number of points of each type by 0.25. To quantify the abundance of certain key tree species known to be important for nesting and feeding, all individuals of the target species more than 2.0 m in height were counted on each territory. We also counted the number of each target tree species within a 3.0-m radius of each grid point to obtain a habitat-specific measure of tree abundance and to evaluate the dispersion of the resource. Target species included fruiting trees important during the dry season (*Acacia collinsii, A. cornigera, Curatella americana*), mass-fruiting trees (*Ficus* spp.,

Spondias mombin), trees that produced fewer fruit that ripened over long periods (*Byrsonima crassifolia, Muntingia calabura*), and trees frequently used for nesting (*Acrocomia vinifera, Crescentia alata*). Counts of the two acacia species were lumped, counts of the remaining fruiting trees were combined into a variable called "other fruit trees," and the two nest-tree species were combined into a variable called "nest trees." Tree abundance was expressed as both the number of trees per territory and as tree density by dividing the number of trees by the area of the territory.

Foraging success.—Timed focal foraging samples of adults (individuals more than 500 days postfledging) and juveniles (independently foraging birds 75 to 500 days postfledging) were performed in a subset of groups during mornings of both the dry and wet season (see Langen 1996a). An individual's behavior was sampled for a cumulative period of 30 to 60 min (timed only when the animal was in sight). Magpie-jays are relatively tolerant of humans, so most observations could be made at a distance of 10 to 25 m.

During a focal sample, we continuously recorded a bird's activity and the habitat type. Foraging was defined as scanning the environment while perched, hopping through vegetation or on the ground, and manipulating substrates or handling prey. The type of each food item was recorded if known, and food items of nonfocal birds also were recorded when observed. From these observations, we calculated the harvest rate (food items per minute foraging) of arthropods (caterpillars and other arthropods) and fruit (all fruit including acacia). Only samples in which the focal bird foraged for a total of five or more minutes were included in the analyses. We then calculated the residual harvest rate for each observation after statistically removing the significant effects of season and, for juveniles, age in days postfledging (see Langen 1996a). The median value of these residuals for a group was then compared with group size. It is important to note that "group size" was based on total group size and not some estimate of foraging party size. Magpie-jays traveled in loose aggregations when foraging, and individuals often flew out of sight and then returned to the group.

Statistical analyses.—Variables were transformed as needed before performing parametric statistical tests. Before tests of linear association were made, we examined plots for evidence of nonlinear effects. Means and standard errors are reported throughout the paper. Probabilities are two-tailed.

Besides examining the simple correlations among group size, group reproductive success, and territory characteristics, we also used structural-equation modeling (a technique closely related to path analysis) to explore the relationships among these variables. This approach has the advantage over classical path analysis (or a hierarchical series of multiple regressions) in that it provides an overall statistical measure of goodness of fit for a hypothesized chain of relationships among variables and allows the investigator to make quantitative comparisons among alternative models (Johnson et al. 1991, Mitchell 1992). We used the EQS computer application from BMDP Statistical Software, which employs an iterative maximum likelihood procedure to compute the path coefficients for a particular model (Bentler 1993). The procedure also identifies nonsignificant variables that should be removed from the model and suggests additional variables that should be added. We first established the hypothesized causal paths and those paths that we knew to be true because some variables were derived from combinations of others. Paths were then added or deleted as suggested by the program until the best possible model was obtained, i.e. all paths leading to dependent variables were significant, the residual error of predicting dependent variables was low, and a comparative fit-index was high. This index measures how well the model accounts for the observed correlations among variables and is scaled from 0.0 (no fit) to 1.0 (perfect fit; Bentler 1990). A maximum likelihood chi-squared statistic representing the difference between the observed correlations among variables and correlations predicted by a model was calculated; if this statistic was nonsignificant, the model adequately accounted for the observed correlations among variables (Bentler 1993). The difference in the chi-squared statistics of two models was used to test for significant differences between them in accounting for the original correlations (see Johnson et al. 1991).

RESULTS

Foraging success and group size.—Groups spent proportionately more time foraging in woodland (i.e. less in pasture) during the wet season than during the dry season (wet season, $\bar{x} = 0.85 \pm$ SE of 0.018%; dry season, $\bar{x} = 0.55 \pm 0.071\%$; Wilcoxon test, $T = 0$, $P < 0.02$, $n = 6$ groups). Adult diets were not significantly different among groups but were significantly different between seasons, primarily because more caterpillars were harvested in the wet season and more acacia in the dry season (log-linear model with group, season, and diet category; 493 to 948 food items per group for six groups, miscellaneous category excluded; $\chi^2 = 38.5$, df = 15, $P < 0.0001$; season and diet category, $\chi^2 \geq 18.5$, $Ps < 0.001$; group, $\chi^2 = 3.6$, $P > 0.05$; Fig. 1).

The harvest rate of arthropods by juvenile magpie-jays was significantly higher in large groups ($r_s = 0.78$, $n = 8$, $P < 0.04$), but the har-
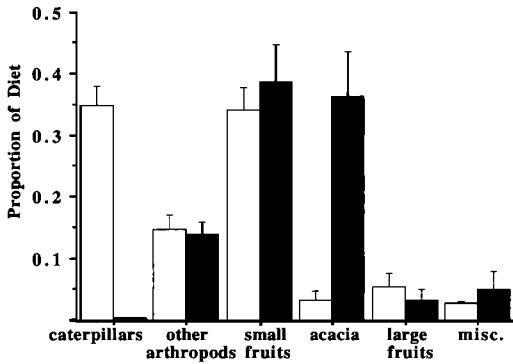
FIG. 1.   Diet of White-throated Magpie-Jays ($\bar{x} \pm$ SE) during the wet (open bars) and dry (closed bars) seasons based on all food items harvested by adult group members during foraging samples, 1991 to 1993 ($n = 6$ groups).

vest rate of arthropods by adults did not vary with group size ($r_s = -0.04$, $n = 9$, $P > 0.50$). Adults tended to have a lower harvest rate of fruits in large groups ($r_s = -0.60$, $n = 9$, $P < 0.09$). The harvest rate of fruits by juveniles was in the same direction but also was not significant ($r_s = -0.38$, $n = 8$, $P > 0.30$).

Territory size and quality, group size, and reproductive success.—Group size varied much more among groups than within groups during the three years that the 14 groups were monitored (one-way ANOVA; among-group MS = 7.1, within-group MS = 1.4; $F = 5.1$, $P < 0.0001$). A two-way ANOVA with group and year as factors did not reveal any consistent year effect; group size fluctuated slightly from year to year with the death, dispersal, or recruitment of group members but was consistently large or small for a given territory. There was no significant difference in the number of disappearances between members of small groups (3 to 5 members, 2 of 41 disappeared) and large groups (6 to 9 members, 3 of 55 disappeared; Fisher's exact test, $P > 0.90$). Group reproductive success, however, varied much more among years than among groups (two-way ANOVA; among-year MS = 2.3, $F = 8.7$, $P < 0.0005$; among-group MS = 0.3, $F = 1.0$, $P = 0.48$). For most groups, reproduction was good in 1992 ($\bar{x} = 2.2 \pm 1.4$ fledglings per group) and poor in 1991 ($\bar{x} = 1.1 \pm 1.1$ fledglings). The coefficient of variation (CV) for group reproductive success among territories (39.7%) was considerably lower than the values reported by

Stacey and Ligon (1991) for other cooperative breeders.

We did not detect any shifts in territory boundaries among the 14 groups over three years, even though modest changes should have been apparent. After averaging the three years of group size and group reproductive success data, we compared these variables with the ecological characteristics of territories (Table 1). The correlation matrix revealed significant correlations or trends for several variables (Table 2). Group size was significantly correlated with territory area when the effect of a confounding variable (number of acacia trees) was statistically controlled (partial $r = 0.70$, $P < 0.05$), and group size also was correlated with the number of acacia trees when the influence of territory area was removed (partial $r = 0.65$, $P < 0.05$). However, per capita acacia (number of acacia trees / group size) was not significantly correlated with group size when per capita territory area (territory area / group size) was statistically controlled (partial $r = -0.13$, $P > 0.20$), nor was per capita territory area correlated with group size after the influence of per capita acacia was removed (partial $r = -0.26$, $P > 0.20$). Therefore, larger groups had significantly more food resources, but food resources did not vary on a per-capita basis with group size. The number of fledglings per successful nest was correlated with the density of acacia trees ($r = 0.71$, $P < 0.005$). The correlation between group size and number of successful nests per year was positive but not quite significant ($r = 0.52$, $P < 0.06$).

Using structural-equation modeling, we tested the hypothesis that territory size and quality determined group size (Model 1; Fig. 2), and the alternative hypothesis that group size determined territory size and quality (Model 2; Fig. 2). Both models demonstrated good statistical fit, and there was no significant difference between them ($\chi^2 = 3.0$, df = 1, $0.05 < P < 0.10$), although Model 1 had a higher comparative fit index and explained more of the variance than Model 2.

A third model (Model 3; Fig. 2) was the best variant on Model 1 for which the direction of causality was reversed between group size and offspring production. This model had a lower comparative fit index but was not significantly different from Model 1 ($\chi^2 = 3.2$, df = 1, $0.05 < P < 0.10$). In all three models, therefore,

TABLE 1. Group size, group reproductive success (fledglings/group), and territory characteristics of 14 White-throated Magpie-Jay groups, 1991 to 1993. Values are $\bar{x}$, with range in parentheses for group size and fledglings per group.

Group	Group size	Group success	Nests[a]	Fledg-lings[b]	Area (ha)[c]	Wood-land (ha)	Nest (ha)[d]	No. acacias	Density acacias	Other fruit[e]	No. nest trees
Aviary	6.8 (6–8)	3.5 (1–5)	1.3	2.8	12.6	10.2	2.5	1,753	138.7	175	71
Borrachos	5.3 (4–7)	1.7 (0–3)	1.0	1.7	23.5	16.0	7.5	823	35.0	297	106
Cafetal	5.0 (5–5)	1.0 (0–2)	0.5	2.0	17.3	16.3	1.3	1,270	73.6	231	72
Caja	4.3 (4–5)	1.8 (1–2)	1.0	1.8	13.0	7.7	4.3	672	51.7	177	83
Camping	8.0 (6–10)	1.5 (0–5)	0.8	2.0	22.5	12.6	9.8	2,341	104.2	89	494
Casona	5.5 (5–6)	2.5 (2–4)	1.3	2.0	13.7	4.6	9.1	1,749	127.8	462	202
Cerca	8.0 (7–9)	2.5 (0–5)	1.0	2.5	27.7	12.6	15.1	3,123	112.6	81	368
Chiringon	4.0 (3–5)	1.0 (0–2)	0.5	2.0	19.0	7.0	11.9	1,079	56.9	104	276
Comedor	5.8 (5–8)	2.8 (0–5)	0.8	3.7	15.1	4.9	10.2	1,740	115.3	190	133
Laguna	5.3 (4–6)	1.3 (0–4)	0.7	2.0	15.5	6.5	9.0	954	61.5	285	63
Rosa Maria	3.3 (2–5)	1.3 (0–4)	0.3	4.0	10.6	5.3	5.3	1,407	134.0	49	134
San Emilio	6.5 (6–7)	1.3 (0–2)	0.8	1.7	30.5	23.0	7.5	754	24.7	199	42
Skippers	5.7 (4–7)	1.7 (0–4)	1.0	1.7	21.0	14.0	7.0	1,193	56.8	128	147
Valle	6.8 (6–8)	2.3 (1–3)	1.0	2.3	20.3	18.5	1.8	922	45.5	147	62

[a] No. successful nests per year.
[b] No. fledglings per successful nest.
[c] Area of territory.
[d] Area of nesting habitat (pasture and park).
[e] No. of other fruit trees.

group size covaried significantly with the number of successful nests, but the direction of causality was unclear. Other factors, including territory area and the number of fledglings per nest, may have affected the number of successful nests per year, but these relationships were not supported in all models. Territories with higher resource densities produced significantly more fledglings per successful nest according to all three models, but group size had no significant effect.

Nesting habitat.—Most nests were located in isolated trees in the middle of a pasture or near human dwellings. Jays may have chosen these sites because the risk of predation by *Cebus capucinus* monkeys (the animals most frequently implicated in nest depredation) and other arboreal predators was lower (Fedigan 1990, Langen 1994). There was a negative trend between area of nesting habitat (park and pasture) and the proportion of nests that failed during a breeding season ($r_s = -0.74$, $n = 7$, $P < 0.08$). The number of nest trees and the proportion of failed nests were not significantly correlated ($r_s = -0.43$, $n = 7$, $P > 0.20$), and neither the amount of nest habitat nor the number of nest trees covaried significantly with group size (Table 2).

Territory boundaries and resource dispersion.— Territory boundaries were drawn onto a map of

the study area that showed the dispersion of the two main habitat types (i.e. pasture and woodland; Fig. 3). Magpie-jay territories consisted of either a patch of pasture surrounded by woodland (e.g. Chiringon and Valle) or a strip of forest and a section from an extensive expanse of adjacent pasture (e.g. Aviary and Cerca). Relatively large pasture areas were defended as parts of territories in regions composed primarily of pasture with small woodland patches (e.g. Laguna, Caja, and Aviary). Where a large patch of pasture was adjacent to a large tract of woodland, the pasture was more finely subdivided (e.g. San Emilio and Borrachos). Territories were not contiguous where large continuous expanses of either pasture or woodland occurred. These patterns suggest that magpie-jays require two different habitat types and that the location of territory boundaries is influenced by the distance between patches of pasture and the resulting amount of interstitial woodland area.

Bull-horn acacias may have been a limiting food resource during the dry season, especially from April to early May when little alternative food was available (Fig. 1). Acacia fruit was also fed to nestlings during this period. Acacias produced a few ripe fruits at a time ($\bar{x} = 4.1 \pm 0.62$ per tree, range 0 to 53, $n = 151$). These trees occurred in both woodland and pasture

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TABLE 2. Correlations between group size, group reproductive success (no. fledglings per group), and territory size based on variables in Table 1.[a]

	Group success	Nests	Fledglings	Area	Woodland	Nest	No. acacias	Density acacias	Other fruit	No. nest trees
Group size	0.472*	0.516*	-0.106	0.598**	0.489*	0.229	0.529*	0.089	-0.023	0.264
Group success		0.761***	0.371	-0.183	-0.182	0.022	0.435	0.463*	0.154	0.066
Nests			-0.314	0.141	0.161	-0.006	0.100	0.000	0.469*	0.001
Fledglings				-0.530*	-0.523*	-0.004	0.487*	0.709***	-0.454	0.091
Area					0.755***	0.381	0.010	-0.570**	-0.029	0.103
Woodland						-0.289	-0.225	-0.621**	-0.021	-0.263
Nest							0.435	0.137	-0.169	0.698***
No. acacias								0.816***	-0.343	0.706***
Density acacias									-0.267	0.486*
Other fruit										-0.410

*, $P < 0.10$; **, $P < 0.05$; ***, $P < 0.01$.
[a] See Table 1 for description of variables. Variables are transformed (natural log or square-root) where appropriate. P-values are not adjusted for multiple tests.

habitats (% occurrence at transect points; pasture, $\bar{x} = 18.0\%$, $n = 345$; woodland, $\bar{x} = 26.4\%$, $n = 590$) and were as dense in either habitat (number of stems per occurrence at transect points; pasture, $\bar{x} = 2.59 \pm 0.305$; woodland, $\bar{x} = 2.90 \pm 0.247$; Mann-Whitney test, $Z = -0.72$, $n_1 = 62$, $n_2 = 157$, $P > 0.40$). Tree distribution was significantly clumped (Poisson goodness-of-fit test based on total stem counts at all transect points, $\chi^2 = 717$, df $= 4$, $P < 0.0001$), and several clumps were scattered throughout each territory (Fig. 4). Among territories, however, the number of acacia trees was highly uniform. This occurred because territory size and acacia density were inversely correlated (Table 2). Acacia had the lowest coefficient of variation per territory of any resource we measured (48.4%), and the per capita number of acacias had an even lower coefficient of variation (37.9%).

DISCUSSION

Three main conclusions can be made from these data. First, both group size and acacia density are directly related to group breeding success, but primarily through different components of fitness. Larger groups are associated with more successful nests, and territories containing a higher density of acacia trees produce more offspring per successful nest. Second, group size is larger on territories with more acacia trees, although the number of acacias per individual within a group is approximately equal across all territories. Third, because each territory contains at least two habitat types, woodland and pasture, territory location may be constrained by the dispersion of these habitat types within the landscape.

Territory quality, group size, and breeding success.—Although many studies have found a significant correlation in cooperative-breeding species between group size (and helper number) and the number of offspring produced, it is often unclear whether this result is due to the direct effects of the additional group members or to another factor that influences both variables, namely territory quality (Brown 1987). For example, high-quality territories may provide surplus food to support extra group members and relatively high production of offspring without there being a causal link between group size and reproductive success. Us-

ing structural-equation modeling, we conclude that territory quality and possibly group size affect offspring production. The causal direction of the correlation between group size and the number of successful nests could not be determined, but other data suggest that larger groups attempt significantly more nests per breeding season because helpers care for dependent fledglings while breeders renest, and because plural breeding (more than one active nest at a time) is more common in larger groups (Langen 1994, 1996b). Our conclusions are similar to those for other species in which helper contributions and territory characteristics have been measured (e.g. Grey-crowned Babbler [*Pomatostomus temporalis*], Brown et al. 1978, 1983; Splendid Fairy-Wren [*Malurus splendens*], Russell and Rowley 1988, Brooker and Rowley 1995). It would be interesting to see how group reproductive success changes in the short and long term when food is increased or decreased experimentally in a territory. Our results would predict: (1) an immediate effect on offspring production due to changes in the number of young raised during each breeding attempt, and (2) a slower additional change in offspring production that parallels the changes in group size caused by altered food abundance and recruitment.

Ecological determinants of group territories.—It has long been recognized that recruitment of additional members (usually retained offspring) in group territorial species must place additional demands on the territory's food resources (Schoener 1968, Shank 1986, Brown 1987, Koenig et al. 1992). In addition, when group territories are shown to have surplus food to support auxiliaries (e.g. Komdeur 1992), it is often unclear why higher-quality habitat has not resulted in a higher density of pair territories. In fact, the typical number of helpers in many group-territorial, cooperative-breeding species is small (1 to 2), and for many more (noncooperative) territorial species, all offspring disperse before the next breeding attempt even if breeding opportunities are limited and territorial vacancies are rare. Group size in these species may be constrained to low numbers as a result of increased food depletion when members are added (Brown 1969). To understand why magpie-jay groups that typically consist of six or more adults share territories, one must determine why resource depletion

does not become a serious cost and, given that resources are sufficient to support all group members, why birds do not subdivide territories into smaller breeding units.

Our data suggest that the dispersion of required habitats within the landscape leads to group territoriality in magpie-jays. We propose that territories must contain two habitat types, pasture and woodland, that are distributed heterogeneously in large patches. Magpie-jays nest in pasture, and pasture also provides acacias and other fruits in the dry season. Woodland also provides acacias and is the habitat where caterpillars and fruit are obtained during the wet season. A typical territory may completely encompass a smaller expanse of the two habitat types. Where woodland and pasture are very extensive, territory boundaries are not always contiguous, but at most locations territory boundaries are adjacent, regularly defended, and appear to remain fixed for years. Magpie-jays do not establish territories where large expanses of woodland exist without pasture, or where large areas of pasture exist without woodland. These interstitial areas may help support the substantial number of floaters in this population.

Although the dispersion of habitats may limit the location of territories, our data suggest that one critical dry-season resource, fruits of bull-horn acacias, limit the density of individuals. Probably other food resources on the territory also affect the number of group members that can be supported on the territory, as indicated by the significant correlation between group and territory size when the influence of acacia is factored out. Magpie-jays appear to be distributed on territories in an ideal-free fashion (sensu Fretwell and Lucas 1970) with respect to acacia and territory area. The phenology of acacia (e.g. low fruit density per plant and slow renewal), and the extreme dependence of the birds on this fruit during the dry season, lead to a significant potential for exploitation competition. Presumably, if groups grow too large in relation to the amount of acacia and other food resources, some individuals disperse (see below).

We suggest that ecological factors limit the minimum sustainable all-purpose territory size to one that is larger than the food requirements of a single pair of magpie-jays. The dispersion of two patchy habitat types, pasture
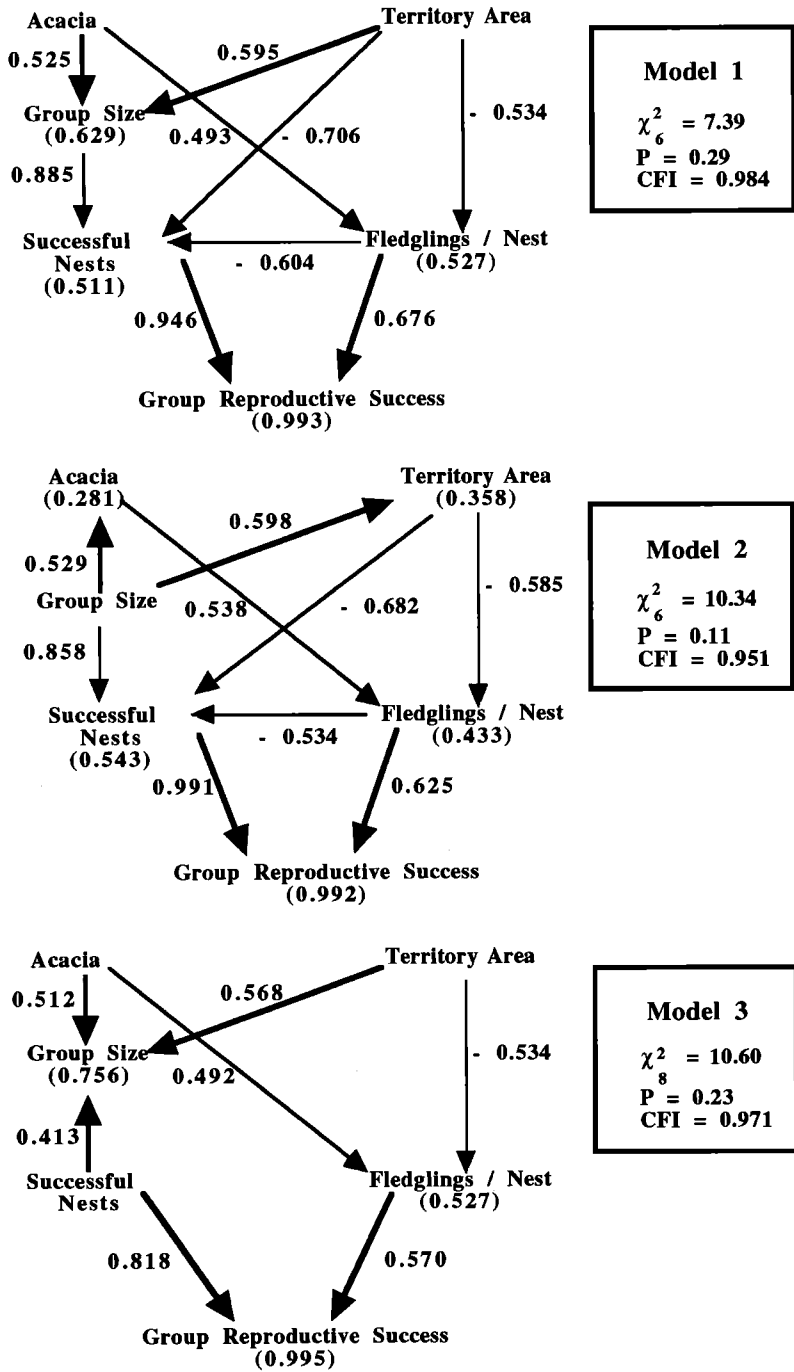
FIG. 2. Path diagrams of possible causal relationships among territory size and quality, group size, and reproductive success. Numbers beside each line are path coefficients (standardized maximum likelihood regression coefficients) from independent to dependent variables (indicated by arrows). Heavy lines are paths fixed at beginning of the analysis, and light lines indicate significant ($P < 0.05$) fitted paths of the final model. For Models 1 and 3, territory size was constrained to determine group size, whereas for Model 2, group size was constrained to determine territory size. Models 1 and 3 differ in the direction of assumed causality be-
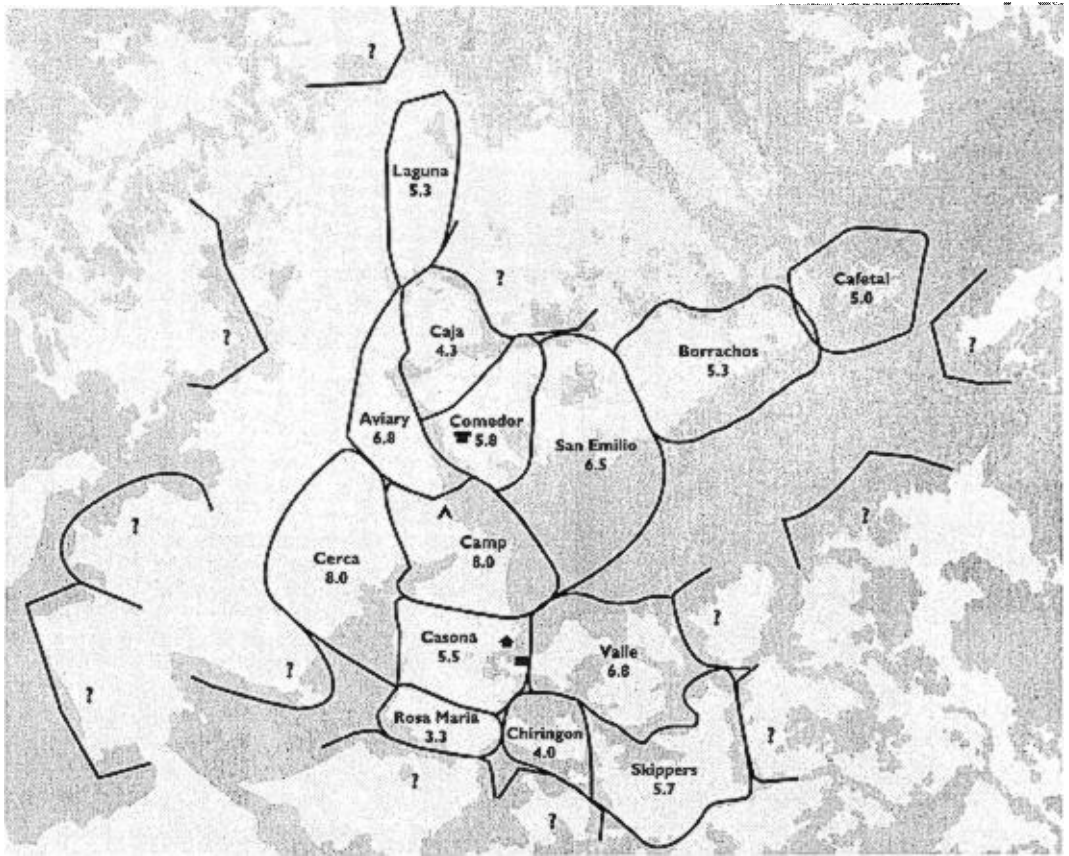
FIG. 3.   Map of study site in Costa Rica showing boundaries of 14 White-throated Magpie-Jay territories and approximate boundaries of nearby groups. Dark areas are woodland; light areas are pastures. Numbers are mean group size from 1991 to 1993.

and woodland, constrain where territories can form, whereas food resources, especially the fruits of bull-horn acacias, place a ceiling on the size that groups can attain. These two features appear to limit the density and location of territories and to constrain the size of groups. Resource dispersion in space and time also seems to be a key factor that favors group territoriality in other species (e.g. Bradbury and Vehrencamp 1976, Macdonald 1983, Koenig and Mumme 1987, Waser 1988, Powell 1989, Walters et al. 1992, Davies et al. 1995). We suspect that resource dispersion may play an important role in group formation in many other group-territorial social systems but that the relationships remain undocumented because of inherent difficulties in measuring the relevant resources.

If our hypothesis is correct, then we should be able to accurately predict how magpie-jay group size and territory size would be affected by three kinds of experimental perturbation. First, if food is added on a territory, group size should increase without a corresponding change in territory size. If, however, food availability is reduced, for example by removing some of the acacia trees, then groups should be-

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tween group size and successful nests. Numbers in parentheses below dependent variables are the proportions of variance explained by the model. The χ^2 and corresponding *P*-values and the comparative fit index (CFI) are reported in the box beside each model.
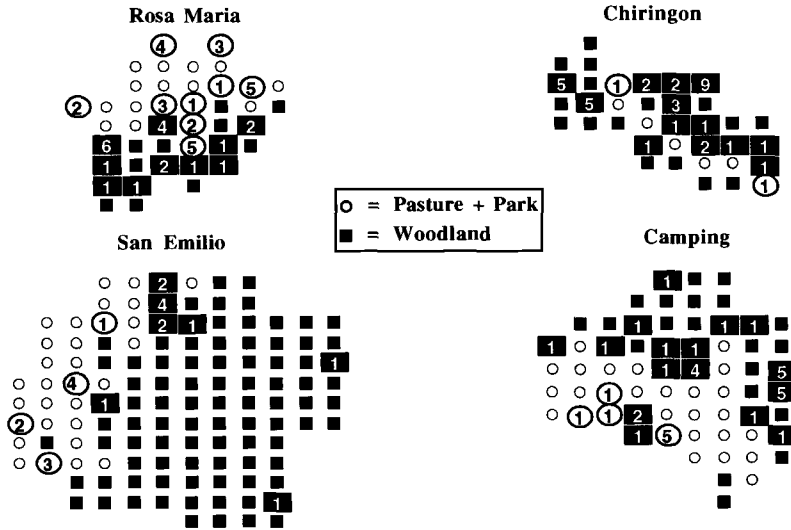
FIG 4. Dispersion of acacias in two small and two large White-throated Magpie-Jay territories based on transect points. Numbers at points represent the total count of acacias >2 m in height within 3 m of the point (i.e. 28.3 m²; interval between points = 50 m).

come smaller, again without a change in territory size. Second, if some group members are removed, survivorship of the remaining jays should not change, nor should territory size change. Eventually, the group should return to the pre-removal size. If an entire group is removed, the area should be reoccupied by a group of similar size that defends territory boundaries corresponding to those of the previous occupants. Finally, if a new area of pasture is cleared within a large area of woodland, a new group should form. If, however, an area of pasture is allowed return to woodland, as is occurring in many areas of Santa Rosa National Park, the territory it supports should disappear. In general, the location and approximate boundaries of territories should be predictable from the dispersion of habitat types such that one could cause the formation or elimination of territories by altering the distribution of woodland and pasture.

The current ranges of the White-throated Magpie-Jay (Pacific slope of Central America from southwestern Mexico to northwestern Costa Rica) and the closely related, cooperative-breeding Black-throated Magpie-Jay (*Calocitta colliei*; northwestern Mexico) closely overlap the region of Mesoamerica that is classified as tropical dry forest (see Janzen 1986). An obvious historical question is whether the behavioral ecology of the White-throated Magpie-Jay

is the consequence of recent landscape changes or whether this species has long been associated with the mosaic of grassland/woodland habitats. Cattle ranching has been practiced near our study site for approximately 400 years (Janzen 1986). Although the original (pre-European) vegetation cover in this region is presumed by some to have been continuous forest, extensive areas of forest were cleared by Mesoamerican farmers thousands of years before the arrival of Europeans (Bush et al. 1992, Denevan 1992). Earlier still, savannas occurred throughout much of the current range of magpie-jays at least until the end of the Pleistocene (Colinvaux 1996). Therefore, the ecological association between these jays and the habitats they currently occupy probably is not recent.

Adjustment of group size.—Mean group recruitment was in excess of group member mortality (0.60 female recruits to adulthood vs. 0.41 female deaths per year per group; Langen [1996b], this study) and was substantially higher than loss of primary breeders (<0.15 primary female deaths per year per group). Survivorship did not appear to vary significantly with group size, but the sample size was small. Survivorship of group members and floaters did not vary significantly (Langen 1996b).

How might group size be adjusted to territory size? Recruitment of offspring probably is sufficient to account for the growth of groups,

but mortality appears to be too low to cause the reduction in group size when groups are too large. Dispersal by some group members is a more likely mechanism of group-size adjustment. Indeed, males disperse from their natal territory at an earlier age when offspring production is high or when group size is relatively large, although all males eventually disperse (Langen 1996a). If our population is near equilibrium, some females also must disperse. Female floaters have been detected (5 to 12% of known-sex floaters; Innes 1992, Langen 1996b), but their proportional representation is less than that predicted from the calculated dispersal rate (0.19 adult females per group per year; hence, 24% of floaters predicted to be female if the primary sex ratio is 1:1 and survivorship is equal for floaters of either sex).

Because territory occupancy was so stable during our study, we do not know the details of how new group territories form. Such knowledge may require the experimental removal of entire groups to determine whether breeding pairs establish territories on vacancies and subsequently add members via recruitment of offspring, whether new groups composed of floaters or nonbreeders from neighboring territories settle on territories, or whether established groups from less-desirable territories settle on better sites.

Causes of cooperative breeding.—Although the dispersion and density of food resources and breeding habitat seem to facilitate the formation of magpie-jay group territories, other factors clearly affect the social system of this species. Breeding vacancies on established territories are uncommon and are filled rapidly (Langen 1996b), and habitat for establishing new all-purpose territories does not appear to exist. The quality of territories as measured directly by the number of acacia trees and territory area, or indirectly by group reproductive success, varies much less than that for the group-territorial species reported in Stacey and Ligon (1991). If, however, undefended areas occupied by floaters are included in a comparison, then habitat quality appears to vary substantially.

Breeders apparently benefit from having some number of helpers because they raise more offspring when more helpers are present (Innes and Johnston 1992, this study). However, at least some of these extra offspring probably

are not the breeders' own, so the magnitude of the benefit provided by helpers is less clear (Langen 1996b). On the one hand, female helpers benefit by remaining in their natal group as helpers rather than dispersing because they augment the production of kin and sometimes gain direct reproductive opportunities (Langen 1996b). On the other hand, males disperse rather than help, perhaps because more reproductive opportunities exist for male floaters than for male helpers (Langen 1996b), and because sufficient vacant habitat exists to support them (although insufficient for establishment of breeding territories).

Finally, there may be additional benefits to being a group member. For example, juveniles appear to benefit as members of larger groups because their rate of harvesting arthropods is higher (this study), perhaps because there are more skilled individuals to provide cues (Langen 1996a). Indeed, all group members potentially may benefit from cues provided by successful foragers (Langen 1996c). Attention to cues provided by group members may be particularly beneficial to White-throated Magpie-Jays because they exploit a variety of different food types that vary dramatically in abundance in time and space (Langen 1996a).

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