

## DISPERSAL IN THE COMMUNALLY BREEDING GROOVE-BILLED ANI (*CROTOPHAGA SULCIROSTRIS*)<sup>1</sup>

BONNIE S. BOWEN,<sup>2</sup> ROLF R. KOFORD<sup>2</sup> AND SANDRA L. VEHRENCAMP

Department of Biology C-016, University of California at San Diego, La Jolla, CA 92093

*Abstract.* We studied dispersal in a color-banded population of the Groove-billed Ani (*Crotophaga sulcirostris*) in Costa Rica. Eight percent of the young alive at the end of the breeding season bred on their natal territories the next year and 4% remained but did not breed. Thirteen percent dispersed successfully within the study area and bred in communal groups or simple pairs. The remaining 75% of the young birds disappeared from the study area. Young males remained in the study area as breeders more frequently than did young females. Breeding dispersal occurred, with at least 9% of the adult population moving to a new territory each year.

We used a demographic model to estimate the following dispersal fates for young birds. For both males and females, 62% of the young alive at the end of the breeding season in which they hatched obtained a breeding position the next year. Of those that dispersed from their natal territories, 59 to 70% of the males and 64 to 74% of the females obtained breeding positions. Of those that bred the year after they hatched, 22% of the males and 2% of the females bred in their natal units, 34% of the males and 6% of the females bred within the study area but outside their natal units, and 44% of the males and 92% of the females bred outside the study area. We estimated that all of the males and 28% of the females that bred the year after they hatched were within three territories of their natal sites.

*Key words:* Groove-billed Ani; *Crotophaga sulcirostris*; *Cuculidae*; Costa Rica; communal breeding; cooperative breeding; joint nesting; dispersal; philopatry.

### INTRODUCTION

In cooperatively breeding birds with helpers-at-the-nest (classification of breeding systems follows Emlen and Vehrencamp 1983), social units often are composed of a breeding pair and their young from one or more previous breeding seasons (reviews in Brown 1978, 1987). In these species young birds delay dispersal for one or more years, or even forego dispersal entirely and become breeders in their natal units. As a result, helpers usually are closely related to the breeders, other helpers, and nestlings in their social unit (Brown and Brown 1981, Woolfenden and Fitzpatrick 1984). In communally breeding species, in which several males or several females breed together, dispersal patterns and relatedness are more variable. In some cases, related individuals breed together (Tasmanian Native Hen, *Tribonyx mortierii*, Maynard Smith and Ridpath 1972; Acorn Woodpecker, *Melanerpes formicivorus*, Koenig and Pitelka 1979; Pukeko, *Porphyrio por-*

*phyrio*, Craig 1979), but in other cases communally breeding individuals are almost certainly unrelated (Galapagos Hawk, *Buteo galapagoensis*, Faaborg et al. 1980).

Groove-billed Anis (*Crotophaga sulcirostris*) are communal breeders in which several pairs build a single nest, have a joint clutch of eggs, and share nestling care (Skutch 1959; Vehrencamp 1977, 1978). Young birds serve as helpers during the season in which they hatch, and most breed the following year. High levels of relatedness among breeders might occur if young birds breed in their natal groups rather than dispersing. We document the dispersal pattern, i.e., dispersal and nondispersal, in a population of Groove-billed Anis and examine the consequences of the observed pattern in terms of group composition and relatedness.

### METHODS

#### STUDY PERIODS AND STUDY SITE

The data reported here are from studies conducted from 1972 to 1973 by Vehrencamp (Vehrencamp 1978) and from 1978 to 1982 by Bowen, Koford, and Vehrencamp. The studies were conducted at Finca Taboga, near Cañas, Guana-

<sup>1</sup> Received 23 March 1988. Final acceptance 7 October 1988.

<sup>2</sup> Present address: Northern Prairie Wildlife Research Center, P.O. Box 2096, Jamestown, ND 58402.

caste Province, Costa Rica. The habitat consisted of pasture, agricultural fields, and second-growth scrub. The study area extended for 10 km along a gravel road. We monitored as many as 60 social units a year, 22 of which were located along the eastern 6 km of the area, one or two territories from the road. The remaining 38 territories were clustered in an area of overgrown pasture. This main area, approximately rectangular in shape, spanned four to six territories in one direction and seven to 10 territories in the other direction. The breeding season lasted from June through December, which corresponded to the wet season. Anis did not breed from January through May, the dry season. From 1978 to 1982 we were present at the site during the following periods: April to December 1978, March to December 1979, March to December 1980, June to December 1981, and June to December 1982.

#### TRAPPING

Most adult anis were captured in traps that contained a pair of hand-raised lure birds (cf. Vehrencamp 1978). Birds either entered the trap or were caught in monofilament leg nooses placed around the outside of the trap. A total of 269 birds was captured: 27 in 1978, 110 in 1979, 63 in 1980, 3 in 1981, and 66 in 1982. We measured and banded each bird, and determined the sex and relative age. Sex was determined using measurements of weight and bill height (males tend to be larger; Vehrencamp 1978). Laparotomies were performed on birds whose measurements fell in the range of overlap. The birds were individually marked with colored plastic leg bands. Because females were difficult to trap, most social units were not completely banded.

#### GENETICS

We collected organ tissues and blood from 19 birds in May 1978 and blood samples from 177 birds in 1978 and 1979. Our initial electrophoretic analysis of 19 individuals for 35 loci yielded eight (23%) polymorphic loci. Three of these polymorphic loci were assayed from blood, but subsequent analysis of blood samples from 177 individuals revealed no genetic variation. Our measures of genetic relatedness therefore are based on pedigrees, not electrophoretic data.

#### BANDING AND CENSUSES OF YOUNG

Nestlings were banded 5 to 6 days after hatching, with narrow bands of the same diameter as the

adult bands. Weight and wing length were recorded. The sex of nestlings was not determined. Bands were placed at this time because nestlings older than 6 days leave the nest if disturbed by humans or a predator. If undisturbed, young leave the nest about 10 days after hatching and spend 10 to 15 days in the vegetation near the ground before becoming volant at about 20 days.

We identified and counted banded young at 1 month of age and irregularly thereafter during the remainder of the breeding season. At the end of the breeding season, all birds on each territory were identified. These final censuses were conducted in early December (1978, 1979), or between mid-November and early December (1980–1982). The young of the year that were present and at least 1 month old during the final censuses are classified as independent young in our analyses. Young from clutches hatched very late in the breeding season, possibly facing relatively high rates of mortality, were thus excluded from most analyses. In addition to the 196 independent young, 14 birds remained in the study area but were not classified as independent young; nine had been too young at the time of the year-end censuses and five had not been observed in the censuses.

#### DEFINITION AND MEASUREMENT OF DISPERSAL

We define dispersal in this paper as the movement of individuals from their territories, excluding temporary forays. Natal dispersal is the movement from a natal territory; breeding dispersal is the movement of an adult from its breeding territory. Dispersers may die in the process of dispersing or may settle on a new territory, in which case they are called successful dispersers. Emigration and immigration refer to the movement of individuals out of and into the study area.

Young anis can acquire breeding opportunities by remaining in their natal units or by dispersing. Censuses of independent young in their natal units during the nonbreeding season were conducted during March through July of 1979 and 1980. For independent young that dispersed successfully within the study area, we determined the size of their breeding units and their breeding roles (for those in groups) during the first nesting attempt of their breeding unit. Breeding units comprise the breeding members of social units, and can be pairs or groups.

### DISPERSAL DISTANCES

Dispersal distances are presented as the number of territories moved, for successful natal dispersers that bred in the study area. The study area was limited in size and the surrounding area was not searched systematically for dispersers. The observed dispersal distribution, therefore, could be truncated and biased (Barrowclough 1978). To obtain a less biased estimate of the dispersal distribution for distances of zero to three territories, we corrected the observed distribution by dividing the number of observations for each dispersal distance by an estimate of the probability of detection for each. We estimated the probability of detection for each distance from the natal territory by calculating a weighted mean of the proportion of territories that were censused for marked birds for that distance. The numbers of independent young produced on each territory during the 5-year study were used as weights. The proportion of censused territories for each distance was obtained by dividing the number of censused territories by the number of territories, if we knew the territorial boundaries, or the number of territories in a packed hexagonal arrangement, if we did not know all of the boundaries (the usual case). We used 6, 12, and 18 as the number of territories at distances of 1, 2, and 3 territories from a natal territory. The estimated probabilities of detection for distances of 1, 2, and 3 territories were 0.65, 0.23, and 0.18. Due to small sample sizes, the corrected frequencies of the two highest classes (2 and 3 territories) were averaged and the mean frequency (0.20) was used for both.

### RADIO TRACKING

In 1979 and 1980, 21 young birds were captured between 6 April and 24 May and fitted with miniature radio transmitters (model SM-1, AVM Instrument Company, Dublin, California). We captured birds by trapping groups known to have had young in the previous year and that still had a large number of birds present at the time. We usually trapped in groups with unmarked young, as we did not want to expose banded young to the risks of carrying radios. A radio was mounted on the back of each bird using a cloth harness (see Vehrencamp and Halpenny 1981 for details). Each bird was checked daily to determine the date of dispersal. Due to technical difficulties, we were able to monitor dispersal from the study

area by only one bird. Of the remaining birds with radios, six died due to complications of carrying the radios, nine survived until July (after the dispersal season) in the groups in which they were captured, and five disappeared.

### BREEDING ROLE IN THE GROUP

Adult members of ani groups differ in their behavior during breeding attempts (Vehrencamp 1977, Vehrencamp et al. 1986). Females can be distinguished based on the order in which they initiate laying in the first nest of the season. In a typical two-female group, one female lays one to four eggs before the second female begins to lay. Before laying, the second female visits the nest and rolls or tosses the eggs of the first female onto the ground. Only the eggs of the first female are tossed (Vehrencamp 1977). We determined laying order by observing females as they laid eggs and by characterizing the eggs of each female by measuring their length and greatest width and describing their shape and coloration. Based on these characteristics and periodic visits to nests, we determined laying order for nests for which we knew which eggs were tossed (the first layer's eggs) or which egg was the first one not tossed (the second layer's egg). Males were distinguished based on their nocturnal incubation behavior; one individual male in the group consistently incubates the eggs at night (Vehrencamp 1977). The nocturnal incubator was determined by watching nests at nightfall to see which bird was incubating and by watching nests at dawn to see which bird left the nest.

### ADULT DISAPPEARANCES

Disappearances of adults may be due to death or breeding dispersal. We present a range of estimated mortality rates for adults, depending on the criteria for attributing disappearances to death or breeding dispersal (Koford et al. 1986). The maximum estimated annual mortality rate of 34% was obtained when all disappearances of marked adults were attributed to mortality. When we attributed disappearances of entire social units to dispersal, we obtained an estimate of 28%. When we also attributed to dispersal the disappearances of mated pairs or of individuals after the prior disappearance of a mate, we obtained a minimum estimate of 22%. For comparisons of mortality rates of adults and young birds, we have used the intermediate figure of 28%, which is in the middle of the range and allows for some

breeding dispersal (see Results section on Breeding Dispersal). The annual mortality rate was calculated from separate estimates of mortality during the breeding and nonbreeding seasons. We calculated the intermediate estimate of mortality as follows: breeding season mortality = 17% ( $n = 433$  bird years); nonbreeding season mortality = 13% ( $n = 251$  bird years). The annual mortality rate, 28%, was calculated by taking the complement of the product of the seasonal survival rates [ $1 - (0.83 \times 0.87)$ ].

## RESULTS

### DISAPPEARANCES DURING THE FIRST YEAR

Most individuals disappeared during the breeding season in which they hatched. Of 399 birds banded as nestlings at about 5 days of age, 274 (69%) disappeared before 30 days of age. Disappearances of young birds during the first 30 days were presumably due to death rather than emigration from the study area, because the young cannot feed themselves during most of this period. The disappearance rate was much lower in the second month of life. Of 103 birds alive at 30 days, seven disappeared before 2 months of age and 96 survived on their natal territories. This disappearance rate, about 7% per month, was not significantly different from the estimated adult mortality rate during the breeding season, about 3% per month ( $G = 2.94, P > 0.05$ ). The disappearance rate was 4% per month for birds 2 to 5 months old (four disappearances for 109 bird months), which was not significantly different from the estimated monthly mortality rate for adults ( $G = 0.012, P > 0.9$ ). We never saw a bird disperse successfully within the study area during the breeding season in which it hatched. The low disappearance rate of young birds more than 2 months old and the lack of observed dispersal lead us to conclude that disappearances of young during the breeding season were virtually all due to death.

Disappearances of birds during their first nonbreeding season could have been due to death in their natal units or to dispersal. Those that dispersed from their natal units may have joined new social units and obtained breeding positions (which we refer to as successful dispersal) or they may have died. To facilitate estimation of the relative amounts of death in situ and dispersal during this period, we restricted our analysis to independent young: birds that had survived the

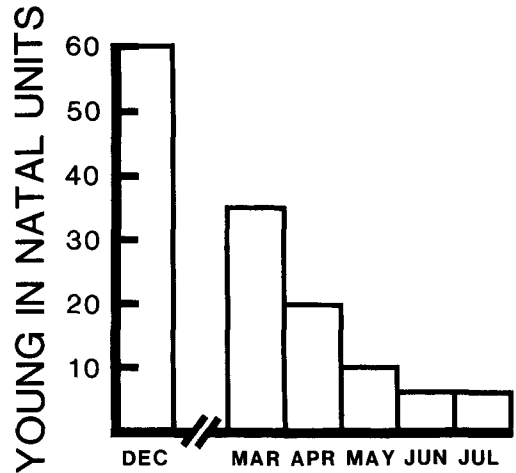


FIGURE 1. Number of independent young that were in their natal units from the end of the breeding season (December) until early in the next breeding season, based on 40 and 20 independent young at the end of 1978 and 1979, respectively.

heavy mortality of the first month of life and survived at least to the end of the breeding season. Very few independent young remained in their natal units at the end of the nonbreeding seasons of 1979 and 1980 (Fig. 1). At the end of March, the time of our first census during the nonbreeding season, 42% of the independent young were no longer in their natal units. Only 12% of the independent young remained in their natal units at the beginning of the subsequent breeding season. Of the 53 birds that did not remain in their natal units, 45 disappeared from the study area, and eight dispersed successfully within the study area.

Were disappearances of independent young due to death or dispersal? Most of the independent young (135 of 162, 83%) studied after 1978 were more than 2 months old at the end of the breeding season. Young birds of this age experienced the same mortality rate during the breeding season as adults. We therefore assume that independent young that remained in their natal units during the nonbreeding season had the same survival rate as adults during the nonbreeding season (87%). Because only 12% of the independent young remained in their natal units (Table 1), we estimate that at least 75% (87% - 12%) dispersed. We estimate the percentage of dispersers that successfully obtained breeding positions in the section on Projected Dispersal Fates.

TABLE 1. Dispersal pattern of independent young the year after they hatched. Numbers and percentages of the number produced each year are shown.

Year	Independent young produced	Disappeared from study area	Dispersed successfully in study area	Remained in natal unit as breeder	Remained in natal unit as nonbreeder
1972-1973	34	26 (76%)	3 (9%)	4 (12%)	1 (3%)
1978-1979	40	31 (78%)	4 (10%)	4 (10%)	1 (2%)
1979-1980	20	14 (70%)	4 (20%)	2 (10%)	0
1980-1981	45	39 (87%)	3 (7%)	3 (7%)	0
1981-1982	57	38 (67%)	11 (19%)	2 (4%)	6 (10%)
Total	196	148 (75%)	25 (13%)	15 (8%)	8 (4%)

#### NATAL DISPERSAL PATTERN

The natal dispersal pattern for independent young was fairly consistent among years (Table 1). Of the 12% of the independent young that remained in their natal units, two-thirds had mates and either bred or attempted to breed. We have analyzed these cases more fully in the sections on sex bias, breeding roles, males in their natal units, and relatedness. Eight independent young remained in their natal units as nonbreeding helpers (Table 1). We observed six additional cases of nonbreeding helpers among individuals that had been too young to be classified as independent young the previous December. Many of these very young birds appear to have postponed dispersal for a year, as none of the four for which we had 2 years of data remained in its natal unit a second year. In contrast, individuals that bred in their natal units sometimes bred there in subsequent years as well. Of nine natal unit breeders for which we had data for two or more years, four were in their natal units or on their natal territories for at least two breeding seasons, two dispersed successfully within the study area in the second year and three disappeared.

Of the 48 independent young that remained in the study area in the year after they hatched, 25 dispersed successfully from their natal sites (Table 1). We presume that they all obtained breeding positions in their new social units. Nineteen are known to have bred. We did not observe the other six closely enough to determine whether they bred or not. Birds usually dispersed individually. Nest mates of the same age were never known to disperse together, as is common in some other communal breeders (Koenig and Pitelka 1979).

Individuals sometimes returned to their natal units after first dispersing. Two of the 25 (8%) successful dispersers, and four independent young

that disappeared from the study area, returned to their natal units during the same breeding season or during the subsequent nonbreeding season. At least three of the six that returned bred in their natal units during the next breeding season. Only one individual first attempted to breed in its natal unit and later, in the same breeding season, dispersed successfully within the study area.

We documented one case of long-distance emigration. This case is not included in Table 1 because the individual did not meet our criteria for classification as an independent young. A female disappeared from her natal area 1 week after she received a radio in 1979. Five days later her radio signal was detected outside the study area, and 5 days after that we found her in a group of four about 6 km from her natal area. She behaved as though she was paired and we observed no aggressive behavior toward her. When observed 17 days later, she again appeared to be a member of the group and we removed her radio.

#### SEX BIAS

Most of the independent young that remained in the study area were males (Table 2). We tested the expectation that equal numbers of males and females bred in their natal units and dispersed within the study area. More males than females bred in their natal units ( $\chi^2 = 5.63$ ,  $df = 1$ ,  $P < 0.05$ ) and dispersed successfully within the study area ( $\chi^2 = 5.78$ ,  $df = 1$ ,  $P < 0.05$ ). The tendency to remain in the natal unit as a nonbreeder was similar for the two sexes. If the sex ratio among independent young in December was 1:1, then more females than males disappeared, suggesting that more females than males emigrated from the study area.

## PROJECTED DISPERSAL FATES

Ideally, in a study of dispersal, one wants to know the fate of all or most of the dispersers. If all cases of successful dispersal are not observed, a demographic model can be used to estimate the proportion of young birds with each of several possible dispersal fates. We probably did not observe all cases of successful dispersal of birds banded in the study area. An indirect method for determining whether some birds dispersed successfully from the study area (i.e., emigrated) is to look for evidence that some birds immigrated and bred. Two lines of reasoning suggest that some birds did immigrate. Direct estimation of the immigration rate was not possible because few of the breeding units were completely banded. The population was fairly constant in size from year to year; for areas studied from 1978 to 1982, the total number of birds censused early in the breeding season had a coefficient of variation of 6.7% (Koford et al. 1986). A constant population size implies that breeding openings created by deaths of adult birds were filled each year. The number of independent young that remained as breeders in the study area was not sufficient to fill all available openings (see below). Immigrants, therefore, must have entered the population. The second line of reasoning concerns the sex bias among individuals that remained in the study area. Because there was no difference in breeding season mortality rates for males (0.17;  $n = 270$  bird years) and females (0.16;  $n = 163$  bird years;  $G = 0.087$ ,  $P > 0.5$ ), we expect the number of breeding openings created by adult mortality to be equal for males and females. Equal numbers of males and females should have filled the breeding openings each year. However, only 12% of the first-time breeders banded as young were females (Table 2). Many of the new female breeders in the population therefore must have been recruited from outside the study area. If, as these two lines of reasoning suggest, individuals have immigrated into the study area and bred, and if the population in the study area was in equilibrium with the surrounding population, then the number of immigrants would be balanced by an equal number of emigrants that bred elsewhere.

To estimate the fates of dispersers, we first estimated the proportion of independent young that bred the year after they hatched. This proportion was estimated by determining the num-

TABLE 2. Dispersal pattern of independent young the year after they hatched, for those that remained in the study area, by sex.

Dispersal class	Males	Females
Dispersed successfully in study area	21	4
Remained in natal group as breeder	14	1
Remained in natal group as nonbreeder	1	1
Total	36	6

ber of breeding openings created by adult mortality and the number of independent young available to compete for breeding positions. In a breeding population of constant size, young birds can breed only if openings are available. For this estimate, we assumed that the individuals that emigrated from our study population entered a population with the same annual rate of adult mortality that we estimated for our population, 28%. This assumption was supported by our finding that breeding season mortality did not vary among years (Koford et al. 1986). We based our calculations of the number of young competing for breeding positions on estimates of reproductive success. Koford et al. (1986) found that for 1978 to 1982, the numbers of independent young produced per adult were 1.19, 0.35, 0.29, 0.58, and 0.25, respectively. There was significant heterogeneity among years and the values were not distributed normally. We therefore summarized these values by the geometric mean, 0.45 young/adult. If we assume that the sex ratio of independent young was 1:1, then for both males and females 45 independent young competed for every 28 breeding positions. On average, the proportion of the independent young that would be expected to breed the year after they hatched was 0.62 (28/45).

We estimated the fates of all independent young (Table 3). In making these estimates we used the following procedure for each sex. First we assumed that 98 of the 196 independent young were males and 98 were females. The proportion expected to have dispersed successfully outside the study area was calculated by subtracting the observed sex-specific proportions that bred in the study area (based on the data in Tables 1 and 2) from the overall proportion of independent young expected to fill breeding openings (0.62, see above). For example, for males, the propor-

TABLE 3. Estimated distribution of dispersal fates of independent young the year after they hatch, based on a demographic model (see text).

	Males	Females
Breeder in the natal unit	0.14	0.01
Successful dispersal within the study area	0.21	0.04
Successful dispersal out of the study area	0.27	0.57
Nonbreeder in the natal unit	0.04	0.04
Death	0.34	0.34

tion of independent young that bred in their natal units was 0.14 (14/98; Tables 1 and 2) and the proportion that dispersed successfully within the study area was 0.21 (21/98; Tables 1 and 2). The proportion that dispersed successfully outside the study area was estimated to be  $0.62 - (0.14 + 0.21) = 0.27$ . Similar calculations were performed for females (Table 3). Of the remaining proportion that did not breed the year after they hatched, some remained in their natal units as nonbreeders and we presume that the rest died. For both males and females, we estimated the proportion that remained in their natal units as nonbreeders to be 0.04 (4/98). In most cases we did not know the sex of the nonbreeders. Because we found no sex bias among natal unit nonbreeders (Table 2), we have divided the eight independent young in this category (Table 1) equally into males and females. We presume the remaining proportion, 0.34, of the independent young of each sex died.

We now return to a question posed earlier and estimate the percentage of dispersers that successfully obtained breeding positions. We have estimated the proportions of independent young that dispersed successfully (Table 3). The estimated proportion that died (0.34, Table 3) may have done so while dispersing or while on their natal territories. If they all died while dispersing, then  $59\% (27\% + 21\%)/(27\% + 21\% + 34\%)$  of the independent young males that left their natal territories dispersed successfully, and  $64\% (57\% + 4\%)/(57\% + 4\% + 34\%)$  of the independent young females that dispersed were successful. It is more likely that some independent young died on their natal territories and never dispersed. In the section on Disappearances During the First Year, we stated that we expected independent young in their natal units to have a mortality rate of 13% during the nonbreeding season. If 13%

of the independent young died on their natal territories, then 21% ( $34\% - 13\%$ ) of the independent young would have died while dispersing. Using this minimum estimate of mortality during dispersal, we estimate that 70% ( $27\% + 21\%)/(27\% + 21\% + 21\%)$  of the independent young males that dispersed were successful, and 74% ( $57\% + 4\%)/(57\% + 4\% + 21\%)$  of the independent young females that dispersed were successful.

Our estimates (Table 3) indicate that an independent young female was about twice as likely to breed outside the study area as was an independent young male. Considering only those independent young that obtained breeding positions, we estimate that 44% of males and 92% of females dispersed successfully outside the study area, 34% of males and 6% of females dispersed successfully within the study area, and 22% of males and 2% of females remained in their natal units.

Due to the wide range of annual variability in reproductive success, there was annual variation in the percentage of young birds that would be expected to breed. In years of low reproductive success, most or all of the independent young would be expected to breed. In the year with the highest reproductive success we observed, approximately 24% of the young birds would be expected to breed.

#### NATAL DISPERSAL DISTANCES

The distribution of natal dispersal distances, from natal unit to the site of the first breeding attempt, is shown in Figure 2 for independent young that bred in the study area the year after they hatched. Figure 2 also shows a corrected dispersal distribution, which is a better estimate of the true dispersal distribution for distances of three territories or less. The fact that the corrected distribution does not approach zero for the longest observed dispersal distance indicates that the entire dispersal distribution was not observed (Barrowclough 1978). Although we do not know the shape of the dispersal distribution beyond three territories, we estimated how much of the distribution was in that part by using information from independent young. We estimate that 62% of the independent young bred the year after they hatched (see section on Projected Dispersal Fates). There were 162 independent young from 1978 to 1982, of which we estimate that 101 ( $0.62 \times 162$ ) bred the year after they hatched. The cor-

rected distribution indicates that 32 of these 101 individuals may have dispersed one to three territories and gone undetected. The sum of this number and the 33 individuals that were observed zero to three territories away is 65, suggesting that 36 ( $101 - 65$ ) individuals may have dispersed successfully beyond three territories.

Most (18/22) of the individuals observed one to three territories from their natal territories were males (Fig. 2). We calculated corrected distributions for each sex, using the detection probabilities as above. We estimate that 41 males and 13 females bred one to three territories away. The sum of 41 and the 10 males that bred on their natal territories is 51, which is approximately the number of males that would have been breeding independent young if the sex ratio were 1:1. We conclude that virtually all of the young that dispersed successfully more than three territories were females. We estimate that 72% ( $[1.0 - (14/50.5)] \times 100$ ) of the female independent young breeding the year after they hatched were more than three territories from their natal territories.

The dispersal distribution (Fig. 2) is based on the independent young that bred the year after they hatched. This distribution is not a complete representation of natal dispersal distances for all birds because two classes of individuals are not included. The first class is the independent young that were nonbreeders in their natal units the year after they hatched. We had breeding information from only one of these, a female that eventually bred on her natal territory. The second class is the adults that had been banded as nestlings but were not classified as independent young. Eight of these were known to breed eventually. Three either bred on their natal territories or dispersed successfully one territory (we could not tell which because the adults in the parental units were not banded), four dispersed successfully one territory, and one dispersed successfully two territories. In the absence of more complete information about dispersal distances of birds that first become nonbreeders and those that hatch late in the breeding season, we consider Figure 2 representative of the natal dispersal distribution for distances of zero to three territories for all birds.

#### BREEDING ROLES OF FIRST-TIME BREEDERS

Of 21 independent young males that dispersed successfully within the study area, 13 bred in

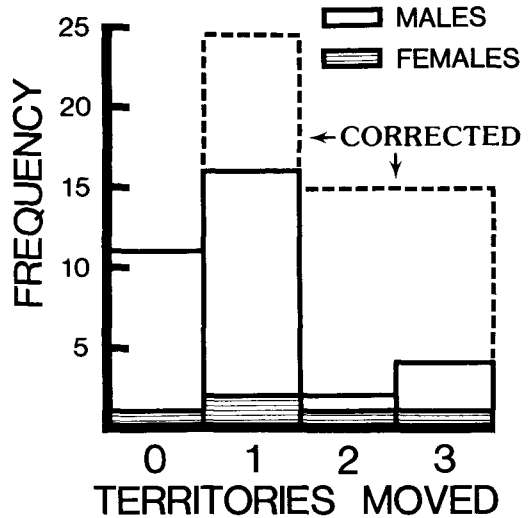


FIGURE 2. Observed distribution of natal dispersal distances of independent young and a corrected distribution based on the probability of detection. The corrected distribution pools the two longest dispersal distances. We estimate that this truncated distribution includes 65% of the young that bred the year after they hatched.

groups and eight bred in pairs. The breeding role was known for six of the group-breeding males; four were nocturnal incubators and two were not nocturnal incubators. Of the 14 males that bred in their natal units, we knew the breeding role for six; none was a nocturnal incubator. Although our sample was small, these data suggest that the role of a male breeding for the first time was influenced by whether or not he was in his natal unit.

The breeding role was unknown for the one long-distance female disperser. The four females that dispersed successfully within the study area all bred in groups. Two were the first layers, and for two laying order was unknown. Only one female bred in her natal unit the year after she hatched. She was the first layer in a nesting attempt monitored in December, but we were unable to confirm laying order during her first nesting attempt of the season.

#### MALES THAT BRED IN THE NATAL UNIT

Males bred in their natal units in two situations, either following the disappearance of a breeding male or when a breeding unit increased in size without the prior disappearance of a breeding male. We analyzed 23 cases in which a group



TABLE 4. Values of Wright's coefficient of relationship,  $r$ , for male and female first-time breeders in various breeding situations.  $r_{YM}$  is the average relationship between a young bird and the other group members;  $r_{MM}$  is the average relationship between all group members.

Category	1. Breeding with parental pair	2. Breeding with natal group	3. Breeding in pair or group of unrelated birds	4. Breeding with siblings or possible siblings
<b>Males</b>				
$n$	3	6	22	3
$r_{YM}$	0.33	0-0.33	0	0.04-0.25
$r_{MM}$	0.25	0-0.17	0	0.02-0.15
<b>Females</b>				
$n$	0	1	4	1
$r_{YM}$		0-0.33	0	0.25
$r_{MM}$		0-0.25	0	0.15

male disappeared. In nine cases young were available within the unit because reproduction had been successful the previous year. A young male remained in the natal unit in four of these cases. Of the five cases in which no young male remained in the natal unit, two of the units disbanded. In the remaining three cases, no male joined the unit. We usually did not know the sex of young birds, and it is possible that no young male was available in some of these five cases. In 14 of the 23 cases, the unit did not produce young that survived until the end of the breeding season. Males from outside the unit joined as breeders in five of these 14 cases and in one case a male that had dispersed the previous year returned to his natal unit as a breeder.

In six cases independent young males remained in their natal units without the prior disappearance of a breeding male. This behavior depended on the initial unit size. Of six simple pairs that had independent young available at the end of the breeding season, three (50%) retained a young male as a breeder the following year and increased the unit size to two pairs. In the 19 cases of units of two pairs with independent young, young males remained in the natal unit three (16%) times. In the five cases of three-pair units with independent young, unit size never increased as a result of young males remaining in the natal unit. These data suggest that a male offspring is likely to remain and breed in situations in which the older breeders are willing to accept a new breeding male and male offspring of the unit are available.

#### MEASUREMENTS OF RELATEDNESS

We calculated the level of relatedness among unit members for breeding units that contained banded birds, using Wright's coefficient of relationship,  $r$  (Wright 1922). In breeding units that contained banded birds that bred in their natal units, we calculated (Brown and Brown 1981) both the average relationship between the natal-unit breeder and the other unit members ( $r_{YM}$ ) and the average relationship between all breeding unit members ( $r_{MM}$ ). The average coefficient of relationship depends on the circumstances in which a bird remains in its natal unit. The three important factors are the number of breeding pairs in the natal unit, whether unit size increased as a result of the young bird remaining in the natal unit, and whether the young bird's mate came from within the unit or not.

In most cases  $r_{MM}$  was lower than  $r_{YM}$ , because the mates of first-time breeders usually were known or assumed to be unrelated to the other members of the unit (Table 4). The highest values of  $r_{YM}$  and  $r_{MM}$  occurred when young birds remained with a parental pair and obtained a mate from outside the social unit. High values of  $r_{YM}$  and  $r_{MM}$  also occurred when an individual bred in its natal unit and obtained a mate from within the unit—possibly a parent. Because a young bird in this situation would have come from a joint clutch, we did not know which adults were its parents, and the range of values reported for category 2 in Table 4 indicates this uncertainty. If an individual bred on its natal territory but obtained a mate from outside the unit, the coefficient of relationship would be lower than the maximum indicated for category 2. It is even possible that a bird would breed in its natal territory but be unrelated to all other unit members if its parents were no longer in the unit.

Most birds that dispersed successfully within the study area were unrelated to the other birds in their breeding units. The 12 males that dispersed and bred in pairs never were known to be related to their mates. An additional 10 males and four females dispersed to join breeding units of three or four birds. In most cases these birds bred with unbanded birds that, most likely, were unrelated to the disperser. If related, they probably would have been distant relatives or sibs from a different year. It is possible that, although unrelated to a banded disperser, some of the unbanded group members may have been related to each other. If so, then  $r_{MM}$  for these units (cat-

egory 3) may have been greater than zero. In one case, two males produced by a group in different years dispersed successfully and bred together in the same unit. Because these birds were produced from joint clutches, we do not know whether or not they were sibs.

Finally, we have estimated that many females dispersed successfully outside the study area. It is most likely that all of these birds were unrelated to all members of the units they joined.

#### INBREEDING

We detected two cases in which inbreeding may have occurred. The first involved a male that remained in his natal unit as a breeder following the disappearance of an adult male, and that mated with the "widowed" adult female (Table 4, category 2). This young bird had hatched from a joint clutch produced by two females. If the female he mated with was his mother, the resulting offspring were inbred. The newly composed group remained stable for the next four breeding seasons and produced several successful clutches. The second case of possible inbreeding involved three sibs, two males and one female, produced by one pair (Table 4, category 4). Two breeding seasons later, after both the parents had disappeared, the unit consisted of the two brothers, their two immigrant female mates, and the sister. This unit of five produced at least two clutches of eggs. The sister was gravid during one of the nesting attempts (the lower abdomen of an ani female about to lay an egg has a characteristic bulge). We conclude that sib-sib mating occurred in this unit. Young were fledged by this unit, but whether any were from the sib mating, and hence inbred, is unknown.

#### BREEDING DISPERSAL

Most birds remained in the same social unit for several years, but some banded adults moved among units. Over the 4-year period 1978 to 1982, during which we monitored 312 bird years, we recorded 29 banded adults moving between units (13 females, 16 males). At least half of these movements were preceded by the disappearance of the bird's mate. The observed annual breeding dispersal rate of 9% provides a minimum estimate, as it is possible that some of the banded adults that disappeared dispersed successfully outside of our study area.

## DISCUSSION

### DISPERSAL DISTANCES

The Groove-billed Ani population we studied was characterized by a high rate of disappearance (75%) of prereproductive birds from the study area during the nonbreeding season. We attribute these disappearances mostly to dispersal from natal units and subsequent emigration from the study area or death within the area. Dispersers apparently had a higher mortality rate than non-dispersers during the nonbreeding season, but we do not know how many dispersers died within and outside the study area. We estimate that many dispersers, especially females, left the study area and bred elsewhere.

How do natal dispersal distances in anis compare with the distances in other cooperative breeders? Without knowing the complete dispersal distribution of the anis hatched in our study area, we cannot make direct interspecific comparisons of the distributions of distances moved by successful dispersers. We can, however, make two indirect comparisons: the estimated percentage of young that bred outside the study area and the estimated percentage of successful dispersers that moved farther than three territories. The problems inherent in making these two comparisons should not preclude us from making them, as long as the results are interpreted cautiously. We realize that the percentages of young that breed outside study areas are not strictly comparable between studies because study areas differ in size and shape. Our main study area, however, was similar in territory dimensions to the three study areas discussed below. The estimated movements of successful dispersers were based on estimated detection probabilities and on an estimate of the proportion of young that bred the year after they hatched.

Two of the most detailed accounts of dispersal in cooperative breeders are for the Stripe-backed Wren, *Campylorhynchus nuchalis* (Rabenold 1985), and the Florida Scrub Jay, *Aphelocoma coerulescens* (Woolfenden and Fitzpatrick 1984). In both studies, the investigators searched for successful dispersers outside the study areas. Rabenold (1985) found in 5 years of study that 9% of the male and 21% of the female first-time breeders that had been banded in his core study area bred outside the area. He was confident that he found most dispersers because of his method of censusing and the fact that the number of em-

igrants from the core area was approximately equal to the number of immigrants. Only 5% of males and 8% of females dispersed successfully more than two territories from their natal territories (data for more than three territories were not given). Woolfenden and Fitzpatrick (1984) found that 2% of the banded males and 17% of the banded females that obtained breeding positions were outside the study area. During their study the rates of immigration and emigration were virtually identical. They found that 4% of the males and 28% of the females successfully dispersed more than three territories from their natal territories.

In studies in which the habitat surrounding the study area is not searched for successful dispersers, one can still observe a part of the dispersal distribution and estimate what proportion of the complete distribution is observed. The common assumptions in these studies are that the number of emigrants equals the number of immigrants and that emigrants from the study area move to a population that is demographically identical to the one they left. To illustrate the power of these assumptions, we used the method outlined by Woolfenden and Fitzpatrick (1984:276) and their data (appendix M) to calculate that one male and nine females would be expected to have dispersed successfully outside their study area. They detected one male and eight females outside the area.

Koenig and Mumme (1987) were unable, as we were, to observe the complete dispersal distribution. In their study of Acorn Woodpeckers in California, they estimated that, of those birds that obtained a breeding territory, approximately 40% of males and 69% of females did so outside the study area. We estimated that for anis that bred the year after they hatched, 44% of males and 92% of females were outside the study area. For both species, the estimated rates of successful dispersal outside the study area are much higher than for the wrens and jays discussed above. We estimated for anis that no males and 72% of the females that bred the year after they hatched were more than three territories from their natal territory. Koenig and Mumme (1987) did not provide comparable estimates for the Acorn Woodpecker. We conclude that natal dispersal distances of female anis hatched in our study area tended to be greater than the distances moved by the male and female wrens and jays discussed above.

Male anis were philopatric, remaining in or

near their natal territories more frequently than did females. We estimated that all young that bred the year after they hatched that were farther than three territories away from their natal sites were females. Differential dispersal between the sexes has been found for many other species of birds (Greenwood 1980, Greenwood and Harvey 1982). Several factors have been proposed to explain patterns of male philopatry and female-biased dispersal in birds. Greenwood (1980) reviewed these factors and concluded that the evidence best supported the hypothesis that male philopatry occurs because males defend a territory, and hence gain an advantage by competing for this resource in a familiar area. This hypothesis may explain male philopatry in the Groove-billed Ani, in which males are more active than females in defending the territory (Vehrencamp 1978). Competitive interactions among individual birds may influence which individuals, both male and female, disperse from the natal unit and which remain near the natal territory. The Oedipus hypothesis (Liberg and von Schantz 1985) is an alternative explanation for female-biased dispersal. Liberg and von Schantz (1985) proposed that adult females are responsible for driving their daughters from the natal territory to prevent brood parasitism. The fact that ani females allow unrelated females to enter the breeding unit and nest jointly suggests that the Oedipus hypothesis does not explain female-biased dispersal in anis.

#### GROUP COMPOSITION AND RELATEDNESS

The dispersal pattern in anis indicates that many young birds were breeding with unrelated birds. Almost all females bred outside their natal units. Young males that remained in their natal units took mates from outside the group. It is likely that some groups consisted entirely of unrelated birds. Over 60% (13/21) of the males that dispersed and bred within the study area were in groups. We observed a few cases of simple pairs coalescing to form a group of two pairs. It is likely that in most of these cases the birds involved were unrelated, although the limited duration of our study may have prevented detection of some cases involving related birds.

One consequence of the observed dispersal pattern was that young males were related to group members more often than were young females. We observed three cases of pairs allowing a male offspring and his unrelated mate to join

the breeding unit the next year. In cases where a male remained in his natal group after an adult male disappeared, the new group consisted of one or both parents, plus one or both members of the other breeding pair from the previous year, usually with an immigrant female mate for the young male. If the original group had consisted of a pair and their son, the new young male would be related to most of the older birds in the group. We observed only two cases of sibs breeding together, although it is possible that short distance dispersals of offspring from successive years into the same group could result in related birds breeding together. Inbreeding may have occurred in this population of Groove-billed Anis, but it was uncommon, as has been found for other cooperative breeders (Brown and Brown 1981, Koenig et al. 1984, Woolfenden and Fitzpatrick 1984, but see Rowley et al. 1986 for a contrasting example).

That young males frequently remained in their natal units when there was a breeding vacancy or when the parental breeding unit was a simple pair is consistent with our understanding of the benefits of communal breeding in the anis. Remaining in the natal unit is probably advantageous to the young male, because he avoids the risks associated with dispersal (predation, finding food in a new area, competing for a territory). Such young males, which were never nocturnal incubators in their natal groups, may also gain a survival advantage over those that disperse and breed in pairs or as nocturnal incubators in groups. Non-nocturnal incubators have been found to have higher breeding season survival than nocturnal incubators (Vehrencamp et al. 1988). However, there may be disadvantages to remaining in the natal group. There is probably an upper limit on group size of three or four pairs, imposed by the number of eggs that can be incubated successfully (Vehrencamp 1977). In addition, per capita reproductive success of groups of three and four pairs may be lower than that of pairs and two-pair groups on territories with little tree cover (Koford et al. 1986). Young birds, therefore, should seldom remain, or be allowed to remain, in groups of two and three pairs because of the reproductive disadvantage that could result. Consistent with this, we found that young males seldom remained in groups of four and never in groups of six unless a breeding male had previously disappeared.

The pattern of retention suggests that groups

that remain on a territory for several years probably will contain relatives. Vacancies created during a year in which at least one young male is available within the group will often be filled from within. Because of the variability among breeding units in the amount of relatedness among group members in the anis, it is not yet possible to compare quantitatively the overall average degree of relatedness among the breeders in ani groups to the average for other communal species. The maximum  $r_{MM}$  for anis (0.25) is similar to that found for Gray-breasted Jays, *Aphelocoma ultramarina* ( $r_{MM} = 0.22$ ; Brown and Brown 1981).

#### ACKNOWLEDGMENTS

We thank the staff of the Centro de Investigación en Biología Celular y Molecular of the Universidad de Costa Rica for assistance during our laboratory studies. M. Frelow provided laboratory collaboration at the Museum of Vertebrate Zoology. Field assistance was provided by B. Brydolf, K. English, G. Loeb, D. Luther, and M. Ryan. We received generous logistical support from the Hagnauer family at Hacienda La Pacifica and E. Sanchez at Finca La Roca. This project was supported by NSF grant DEB 7825230 to SLV, an NIH postdoctoral traineeship (GM-07199) from the Department of Biology, University of California, San Diego to BSB, the National Geographic Society, and the Affirmative Action Program of the University of California, San Diego. We are also grateful for the services of the Computing Centers at UCSD and Idaho State University.

#### LITERATURE CITED

- BARROWCLOUGH, G. F. 1978. Sampling bias in dispersal studies based on finite area. *Bird-Banding* 49:333-341.
- BROWN, J. L. 1978. Avian communal breeding systems. *Annu. Rev. Ecol. Syst.* 9:123-155.
- BROWN, J. L. 1987. Helping and communal breeding in birds. Princeton Univ. Press, Princeton.
- BROWN, J. L., AND E. R. BROWN. 1981. Extended family system in a communal bird. *Science* 211:959-960.
- CRAIG, J. L. 1979. Habitat variation in the social organization of a communal gallinule, the Pukeko, *Porphyrio porphyrio melanotus*. *Behav. Ecol. Sociobiol.* 5:331-358.
- EMLEN, S. T., AND S. L. VEHRENCAMP. 1983. Cooperative breeding strategies among birds, p. 93-133. In A. H. Brush and G. A. Clark, Jr. [eds.], *Perspectives in ornithology*. Cambridge Univ. Press, New York.
- FAABORG, J., T. DE VRIES, C. B. PATTERSON, AND C. R. GRIFFIN. 1980. Preliminary observations on the occurrence and evolution of polyandry in the Galapagos Hawk (*Buteo galapagoensis*). *Auk* 97:581-590.
- GREENWOOD, P. J. 1980. Mating systems, philopatry

- and dispersal in birds and mammals. *Anim. Behav.* 28:1140-1162.
- GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* 13:1-21.
- KOENIG, W. D., AND R. L. MUMME. 1987. Population ecology of the cooperatively breeding Acorn Woodpecker. Princeton Univ. Press, Princeton.
- KOENIG, W. D., R. L. MUMME, AND F. A. PITELKA. 1984. The breeding system of the Acorn Woodpecker in central coastal California. *Z. Tierpsychol.* 65:289-308.
- KOENIG, W. D., AND F. A. PITELKA. 1979. Relatedness and inbreeding avoidance: counterplays in the communally nesting Acorn Woodpecker. *Science* 206:1103-1105.
- KOFORD, R. R., B. S. BOWEN, AND S. L. VEHCAMP. 1986. Habitat saturation in Groove-billed Anis (*Crotophaga sulcirostris*). *Am. Nat.* 127:317-337.
- LIBERG, O., AND T. VON SCHANTZ. 1985. Sex-biased philopatry and dispersal in birds and mammals: the Oedipus hypothesis. *Am. Nat.* 126:129-135.
- MAYNARD SMITH, J., AND M. G. RIDPATH. 1972. Wife sharing in the Tasmanian native hen, *Tribonyx mortierii*: a case of kin selection? *Am. Nat.* 106:447-452.
- RABENOLD, K. N. 1985. Cooperation in breeding by nonreproductive wrens: kinship, reciprocity, and demography. *Behav. Ecol. Sociobiol.* 17:1-17.
- ROWLEY, I., E. RUSSELL, AND M. BROOKER. 1986. Inbreeding: benefits may outweigh costs. *Anim. Behav.* 34:939-941.
- SKUTCH, A. F. 1959. Life history of the Groove-billed Ani. *Auk* 76:281-317.
- VEHCAMP, S. L. 1977. Relative fecundity and parental effort in communally nesting anis, *Crotophaga sulcirostris*. *Science* 197:403-405.
- VEHCAMP, S. L. 1978. The adaptive significance of communal nesting in Groove-billed Anis (*Crotophaga sulcirostris*). *Behav. Ecol. Sociobiol.* 4:1-33.
- VEHCAMP, S. L., B. S. BOWEN, AND R. R. KOFORD. 1986. Breeding roles and pairing patterns within communal groups of Groove-billed Anis. *Anim. Behav.* 34:347-366.
- VEHCAMP, S. L., AND L. HALPENNY. 1981. Capture and radio-transmitter attachment techniques for Roadrunners. *N. Am. Bird Bander* 6:128-132.
- VEHCAMP, S. L., R. R. KOFORD, AND B. S. BOWEN. 1988. The effect of breeding-unit size on fitness components in Groove-billed Anis, p. 291-304. *In* T. H. Clutton-Brock [ed.], *Reproductive success*. Univ. of Chicago Press, Chicago.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Princeton Univ. Press, Princeton.
- WRIGHT, S. 1922. Coefficients of inbreeding and relationship. *Am. Nat.* 56:330-338.