COMMUNAL SOCIAL BIOLOGY OF THE
SOUTHERN SAN BLAS JAY

JOHN WILLIAM HARDY

THOMAS A. WEBBER

AND

RALPH J. RAITT

COMMUNAL SOCIAL BIOLOGY
OF THE SOUTHERN SAN BLAS JAY

JOHN WILLIAM HARDY, THOMAS A. WEBBER,
AND RALPH J. RAITT[1]

SYNOPSIS: We studied the communally-breeding Southern San Blas Jay, *Cyanocorax (Cissilopha) s. sanblasianus*, from 1974 to 1978 near Acapulco, Guerrero, Mexico. In this area it inhabits only palm plantations and the small remnants of native woodland scattered among them. Most nests are built in the crowns of coconut palms.

This jay lives year-round in nonmigratory groups of fairly constant composition, which on our study areas ranged in size from 13 to 26 birds one year old and older. In each group 62-82% of the members were at least 3 years old. Each group contained 6-10 breeding pairs that were probably permanently monogamous, plus a smaller number of nonbreeders. With the exception of replacement nests and the rare occurrence of second broods, female breeders laid in only one nest per breeding season, and only one female laid in each nest.

Breeding pairs were assisted in feeding and defending their young by both the nonbreeders and breeders of their communal group. Some nests were attended by as many as 13 birds. Helpers, whether breeders or nonbreeders, preferred to feed fledglings rather than nestlings. Nests begun earlier in the breeding season attracted more helpers than did later ones, because of the accumulation of fledglings as the season progressed.

The feeding rate per nest increased with brood size, but there was no correlation between the feeding rate per nestling and brood size. The positive correlation between feeding rate per nest and brood size is probably a result not of greater rates of feeding per attendant, but of larger numbers of attendants, each of which feeds at a rate independent of the number of nestlings. All birds of known parentage helped at their parents' nests, though none helped its parents exclusively.

Most birds began breeding at 3 years of age or older, but 1- and 2-year-olds were breeders more commonly than is at present evident in the other three species of *Cissilopha*. Younger breeders tended to nest later in the breeding season than older breeders.

Each communal group inhabited an exclusive home range, whose boundaries with other groups were maintained by mutual avoidance rather than by active defense. In one large group, whose members were dispersed over a comparatively large home range, breeders with active nests confined their activities to a small fraction of their group's home range and exerted a quasi-territorial dominance over other group members who entered these areas. Such individual "core areas" were not evident in smaller groups.

The commonest clutch sizes were 3 and 4. Incubation lasted 17-18 days, and the nestling period was about 18-20 days. Breeding pairs were usually single-brooded. Between 50 and 68% of nests that had clutches produced at least one fledgling, and 22-38% of all eggs resulted in fledglings. From 0 to 50% of young that fledged survived to at least 1 year of age. The annual survival rate of yearling and older birds was about 75% in most years. Changes in group membership, by both young and adults, appear to be of infrequent but regular oc-

[1]John William Hardy is Curator in Ornithology, Florida State Museum, University of Florida, Gainesville FL 32611; Thomas A. Webber is a graduate student in the Department of Zoology, University of Florida; and Ralph J. Raitt is a Professor in the Department of Biology, New Mexico State University, Las Cruces NM 88003

currence. Females seemed to change groups more often than did males. Most of the immigrants to our study groups were of unknown origin.

The movements of dependent juveniles and their attendants are described.

Southern San Blas Jays are omnivorous. They seemed to forage about equally in palms, herbaceous growth, hedgerows, and jungle patches. During the breeding season they did not usually forage in flocks. There was little or no mixing of birds from different communal groups during the nonbreeding season. At that time of year they typically foraged in flocks and were less vocal than in the breeding season.

We speculate on the way in which each *Cissilopha* species' characteristic group size, number of breeders per group, and age at first breeding, may be related to one another and to the productivity of the habitat.

TABLE OF CONTENTS

INTRODUCTION

Four allopatric species of Middle American jays, known as the black-and-blue jays, constitute the subgenus *Cissilopha* of the widespread neotropical genus *Cyanocorax* (see Hardy 1969 for the taxonomic revision that we follow here, which submerges *Cissilopha* in *Cyanocorax*). These four species are the Yucatan Jay, *C. yucatanicus*, of southeastern Mexico and adjacent Belize; the Beechey Jay, *C. beecheii*, of central western Mexico in Sonora and Sinaloa; the Bushy-crested Jay, *C. melanocyaneus*, of Guatemala, Honduras, and El Salvador; and the San Blas Jay, *C. sanblasianus*, of southwestern Mexico.

There are two races of the San Blas Jay. The Nelson San Blas Jay *(C. s. nelsoni)* ranges from the state of Sinaloa south to northern Guerrero, Mexico. The Southern San Blas Jay *(C. s. sanblasianus)* occurs from about 100 km northwest to about 70 km southeast of Acapulco, Guerrero. These two races are separated by about 200 km, and they differ in certain aspects of their vocalizations, softpart color, and plumage (Hardy and Raitt 1977).

We have studied the breeding biology of all four species of black-and-blue jays, including both races of the San Blas Jay (Raitt and Hardy 1976, 1979; Hardy 1976; Raitt et al., ms.). Each of these forms exhibits a variation on the theme of communal social behavior, in which birds live year-round in groups of basically stable composition, and breeding pairs receive assistance from other group members in feeding and defending their young.

Prior to our work, the behavior of these four species in the wild was virtually unknown. These studies help to fill a large Middle American geographical gap in our knowledge of communal New World jays.

Our objective in studying these four species was to determine at least the outlines of their social organization, especially their communal breeding behavior, their demography, and the nature of their habitats. The ethology and systematics of the subgenus were of secondary importance to us.

We decided not to attempt a long-term intensive investigation, such as that being conducted on the Florida Scrub Jay *(Aphelocoma c. coerulescens)* by Woolfenden (Woolfenden and Fitzpatrick 1978 and references therein), of a single species of neotropical jay. We could not conduct such a study year-round from our base in the United States. Also the study areas themselves lead a precarious existence at the mercy of neotropical agriculture and forestry (one of our study sites was razed in the midst of our work), so that we were wary of investing effort in the sort of study that depends on having a site secure from interference for a decade or more. Finally, we felt the urgency of getting some information about each species before it becomes extinct or so rare as to be impossible

to study (this is most likely in the case of the Beechey Jay; see Raitt and Hardy 1979). In short, we decided we would rather have limited information on four species than somewhat more information on only one.

This paper presents our findings on the fifth and final form to be studied in the subgenus, the Southern San Blas Jay. Because of the relative ease with which it could be studied, it yielded richer information than did any of the other black-and-blue jays, showing it to have the most elaborate and peculiar communal breeding behavior of any New World jay studied so far.

ACKNOWLEDGMENTS

MATERIALS AND METHODS

Our principal study site was 13 km northwest of Pie de la Cuesta, Guerrero, about 2 km north of the Laguna de Coyuca. Our other study site was 6 km southeast of Acapulco International Airport, about 2 km inland from Playa Encantada.

We captured, aged, sexed, color-marked, and released jays of four communal groups at the main study site and one group at the other site hereafter called the southern site. Birds were caught in mist nets or by hand.

We determined the birds' ages by criteria of Hardy (1973) and Hardy and Raitt (1977). By using a combination of plumage characters and eye color, one can distinguish in the field between juveniles, yearlings, 2-year-olds, and "adults." Through their second year Southern San Blas Jays have brown eyes. The irides then gradually change through various shades of green until by 3 years of age they are pure yellow and remain so for life. We have found few exceptions to this rule. Since 1977 we have encountered two 2-year-olds with greenish-yellow eyes that at a distance were difficult to distinguish from those of adults. Some 3-year-olds retained a greenish tinge to the eye, which could be distinguished from pure yellow only with the bird in hand. On the whole, age classes remained distinguishable with remarkable reliability.

Sex was determined by a combination of weight, presence of a cloacal protuberance or brood patch, and reproductive role.

The birds were marked with colored plastic tarsal flags ("Saflag") and usually with anodized aluminum or plastic leg bands in the same color combinations. Individual birds are referred to by their color markers, the left leg first. Thus PiG means pink on the left, green on the right and Pi/G-L means pink over green on the left. Colors and their symbols in this paper are: O, orange; Bl, blue; Bk, black; W, white; Pi, pink; P, purple; G, green. An "X" denotes absence of a band. A suffix numeral indicates that the combination was used previously on a bird now presumed to be dead. In each year of the study some birds (usually females) re-

mained unmarked in each group, but usually could be distinguished by a combination of their age, association with a particular site or marked bird, degree of hostility toward humans, and peculiarities of voice. In some cases these characteristics were deemed reliable enough to identify unmarked birds from year to year.

We studied the Southern San Blas Jay in five breeding seasons from 1974 through 1978. Field work in 1974 was conducted from 25 to 30 June by three persons (approximately 16 man-days). Some birds in group 1 were flagged, two nests were found and studied, and the general nature of the main study site and the jays was assessed, including verification of the detectability of age classes in the field.

Field work in 1975 was conducted from 21 June to 28 July by four to six persons (approximately 160 man-days), all at the main study site except for two man-days at the southern site.

Field work in 1976 was conducted from 23 June to 28 July by two to seven persons in approximately 160 man-days (18 days at the southern site).

In 1977 study was conducted from 10 June to 27 July by four to eight persons (appproximately 240 man-days).

In 1978 eight days (18-25 June) were spent by two people censusing the two best-studied communal groups, ascertaining the survival of flagged birds, the size and composition of the groups, and pair bond persistence, with some effort devoted to determining the number of nests, their distribution, timing, and success. From 1975 through 1977 attention was given to netting birds; following flagged birds to detect group membership, individual roles, home ranges, and core areas (subdivisions of home ranges); and to studying nests and fledglings.

Figure 1 is a map of the study site, showing the distribution of vegetation, roads, lanes, fences, and other features.

RESULTS

Nests and Principal Habitat

In the present study, 52 nests were found or were known circumstantially to have existed in the communal groups that we have designated 1, 2, and 3. Of these, 48 were in coconut palms on a bract or cluster of coconuts at the base of the fronds. Two were in the crowns of lime trees and two on bracts of small native palms (species not determined). All nests were within the palm groves and none within the patches of native woodland nearby. Nests ranged in height of placement from 2 m (lime tree) to 18 m. Most of the nests were 9 to 15 m up, the smallest and the very tallest palms rarely being selected as nest trees. Mean height of 39 nests that we were able to measure was 11.8 m.

Certain portions of each group's home range were consistently preferred for nesting from year to year. Figure 2 shows all nests given a number in the main study area from 1974 through 1978. The jays nested in those parts of the groves that satisfied three requirements: (1) the canopy of the palm crowns was not too dense; (2) there were no acacia thickets but lush herbaceous growth instead; and (3) there was native woodland nearby. The frequency with which any fronds of adjacent palms touched (expressed as a percent of the total possible) was used as an index of canopy closure (Table 1). The palms were planted in straight rows and
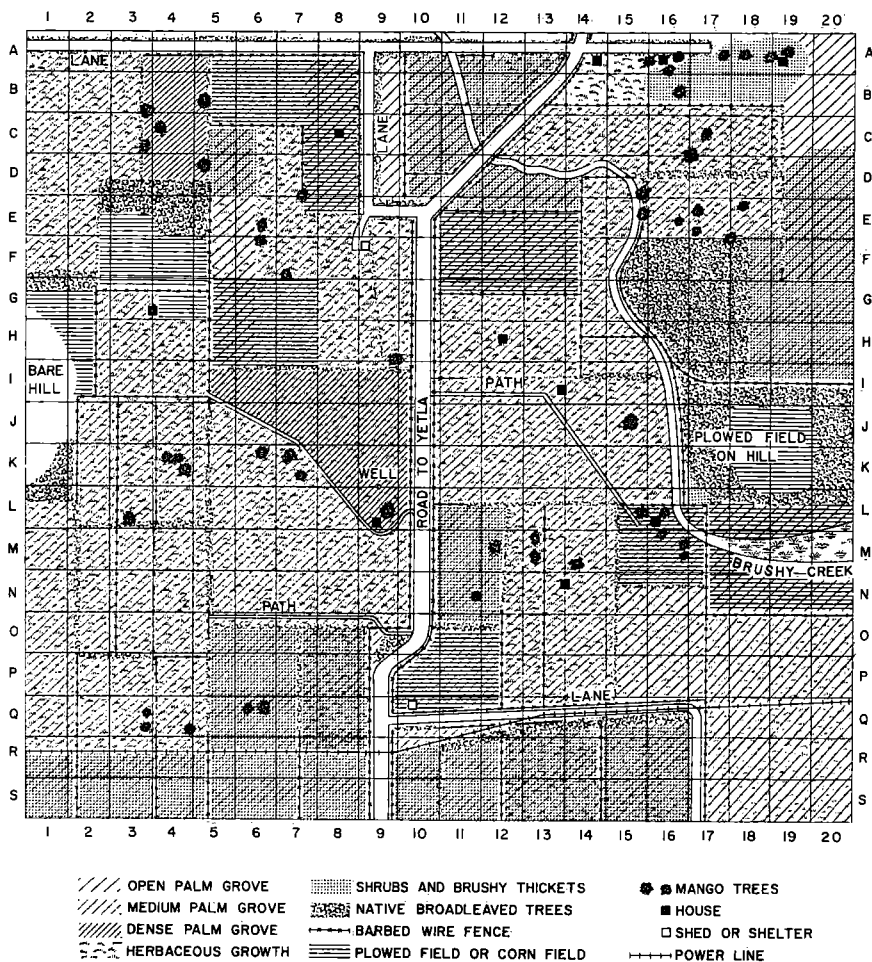
FIGURE 1.   Map of the main Southern San Blas Jay study site, showing landmarks and vegeta-
tion. Areas bounded by coordinates A-B/12-13 and R-S/12-16 have palms and ground level
vegetation of herbaceous growth, shrubs, and brushy thickets.

columns, so that each tree (unless on the edge of the grove) had four
nearest neighbors. Thus, if a given palm touched, say, three of its four
neighbors, its closure index was 75%. The closure index for a sample
quadrat is the mean of the closure indices of all the trees in the quadrat.
Eight square quadrats, each of one hectare, were censused in 1977. Three
of these were selected because they contained jay nests (quadrats 1, 4, 7);
the other five represented habitat variations not used for nesting. The in-
dex of closure for those having nests is 7.2% or less. Of the five having no
jay nests in the five years, three (2, 3, 8) had 10% or greater closure in-
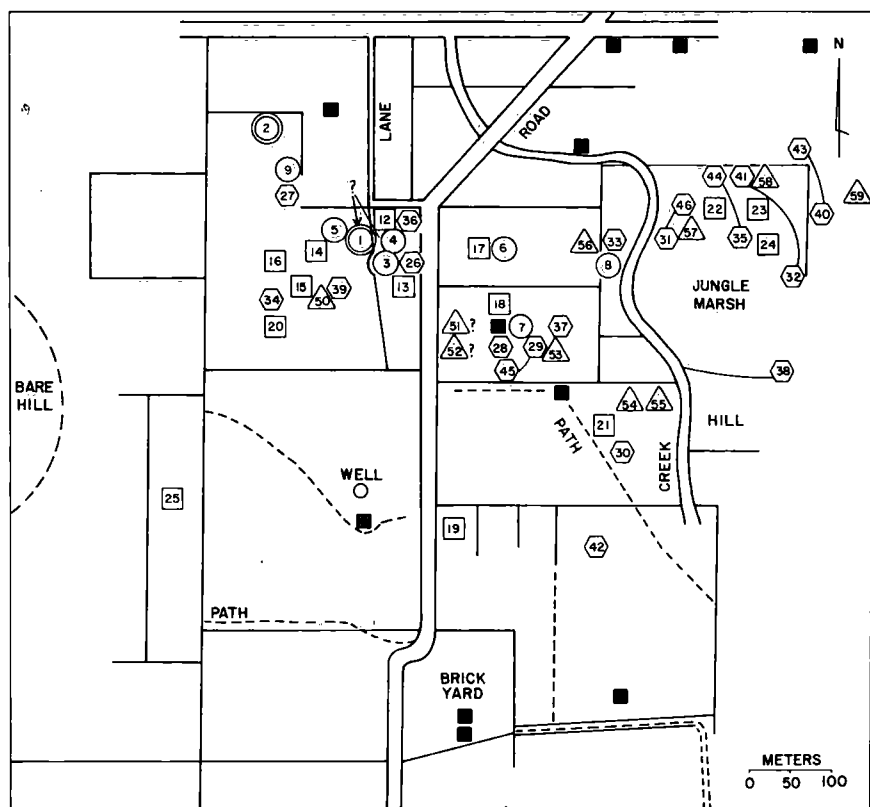
FIGURE 2.   Locations of all known active nests at the main study site, 1974-78. Double circles = 1974; circles = 1975; squares = 1976; hexagons = 1977; triangles = 1978. Nest 1's exact location not ascertained. Approximate positions of nest 51 and 52 indicated by question-marked designations.

dices; one (5) had a low index of 0.17 % ; and one (6) had a 5.3 % closure, was frequented by jays, and probably had nests occasionally. The relatively open-canopied groves may be selected as a means of reducing predation by snakes and squirels. In groves where the trees are far enough apart to prevent a climbing predator from traveling from crown to crown, these animals must return to the ground and ascend each tree. This difficulty may make open groves unattractive to such predators. We rarely saw squirrels in the nest areas, but found them frequently in the groves not used for nesting and having relatively closed canopies, where they moved easily between adjacent trees with intermingling fronds.

Rich herbaceous growth, both for foraging and for the protection it affords fledglings, also is a feature of good nesting groves. Groves with the ground cleared and plowed for corn planting had nests only where

TABLE 1. — Coconut grove quadrat comparisons.

Quadrat number	No. of trees	No. of possible touches	No. of touches	Index of closure	Jay use	Other features
1	156	594	43	7.2	Nests	Ground forbs and hedgerows
2	196	698	133	19.0	Rare forage	Sparse ground cover
3	360	1478	163	11.0	Forage	Sparse ground cover
4	191	984	34	3.4	Nests	Heavy forb cover
5	144	600	1	0.17	No Jay use	Brushy acacia understory
6	144	600	32	5.3	Forage, probably nests previously	Similar to 4 above
7	152	591	31	5.2	Nests	Sparse ground cover, many hedgerows.
8	195	861	87	10.1	No Nests forage	Heavy forb cover

bordering on preferred habitat. The failure of quadrat 5 to have jay nests is possibly related to the brushy acacia growth at ground level. We found no nests where these acacias and shrubs grew in dense thickets.

The jays favored nesting sites near remnants of native broadleaved woodland, either as islands of at least a few hundred m² or as hedgerows in and around a grove. Each communal group seemed to have its own more or less exclusive woodland foraging ground. A particularly striking example of the importance of such tracts was seen in the case of group 4. The hill on the north side of that group's home range (Figs. 1 coordinates 18-19/J-K; 2, 14) was covered with a dense low jungle in 1976. By the time we arrived in 1977, the hill was completely denuded for planting corn. This jungle patch had been the major tract of native vegetation available to group 4 (see Fig. 14). The group had completely disappeared by 1977. By July 1978 the hillside jungle had begun to grow back and birds of group 2 were foraging there, but the palm grove portion of group 4's former home range was never reoccupied by jays of any group.

Figure 3 shows several views of the coconut palm groves the jays inhabited.

OCCURRENCE IN OTHER HABITATS

Northwest of Acapulco we found Southern San Blas Jays nesting only

FIGURE 3.   Vegetation of the main study site. (A) Spotting scope is directed toward nest site (white arrow) in coconut palm. (B) Mango foodtree with overstory of coconut palms, and herbaceous ground cover. (C) Palm at the south edge of the "jungle"—a patch of native broadleaved evergreen woodland—in the group 2 home range.

in palm groves. At the southern site, southeast of the city, a large remnant of coastal plain broadleaved scrub woodland is intermingled with the coconut groves and open corn fields, where, in addition to the adjacent palm groves, we found the jays nesting in the edges of the scrub. This habitat, shown in Figure 4, was very patchy; we found two patches large enough to constitute true woodland and ascertained that the jays were not nesting in their interior. The relationship of the San Blas Jay to the original vegetation is considered further in the Discussion.

COMMUNAL STRUCTURE

GROUP COMPOSITION. — Appendix I summarizes basic information on all the jays studied in groups 1 and 2. Only some of the group 1 birds and none in group 2 were flagged in 1974. Thus the 1974 column of Appendix I does not fully show group 1's composition for that year and is given to show persistence of some individuals throughout later years. The same is true for the 1975 column with respect to group 2. Data on the member-ship of group 1 are complete for 1975-78 and for group 2, 1976-78. Table 2 summarizes the age composition of groups 1 and 2 for the years in which adequate data are available.

Southern San Blas Jays live in groups that are unusually large for com-munal breeders (see Brown 1978). The sizes of the two groups (1 and 2) that we studied most intensively usually were about 14 and 24 respec-tively (Table 2). The three groups (3, 4, and 5) that we studied in less detail never had fewer than 10 birds each.

From 1976 to 1977 the size of group 1 remained unchanged. Group 2 increased in size from 22 to 26 birds by immigration of GPi from group 3 and possibly by recruitment of some unmarked birds from group 4 (although only 22 of these were observed regularly; the remaining four

TABLE 2.—Proportion of age classes (marked and unmarked birds) in groups 1 and 2 of Southern San Blas Jays.

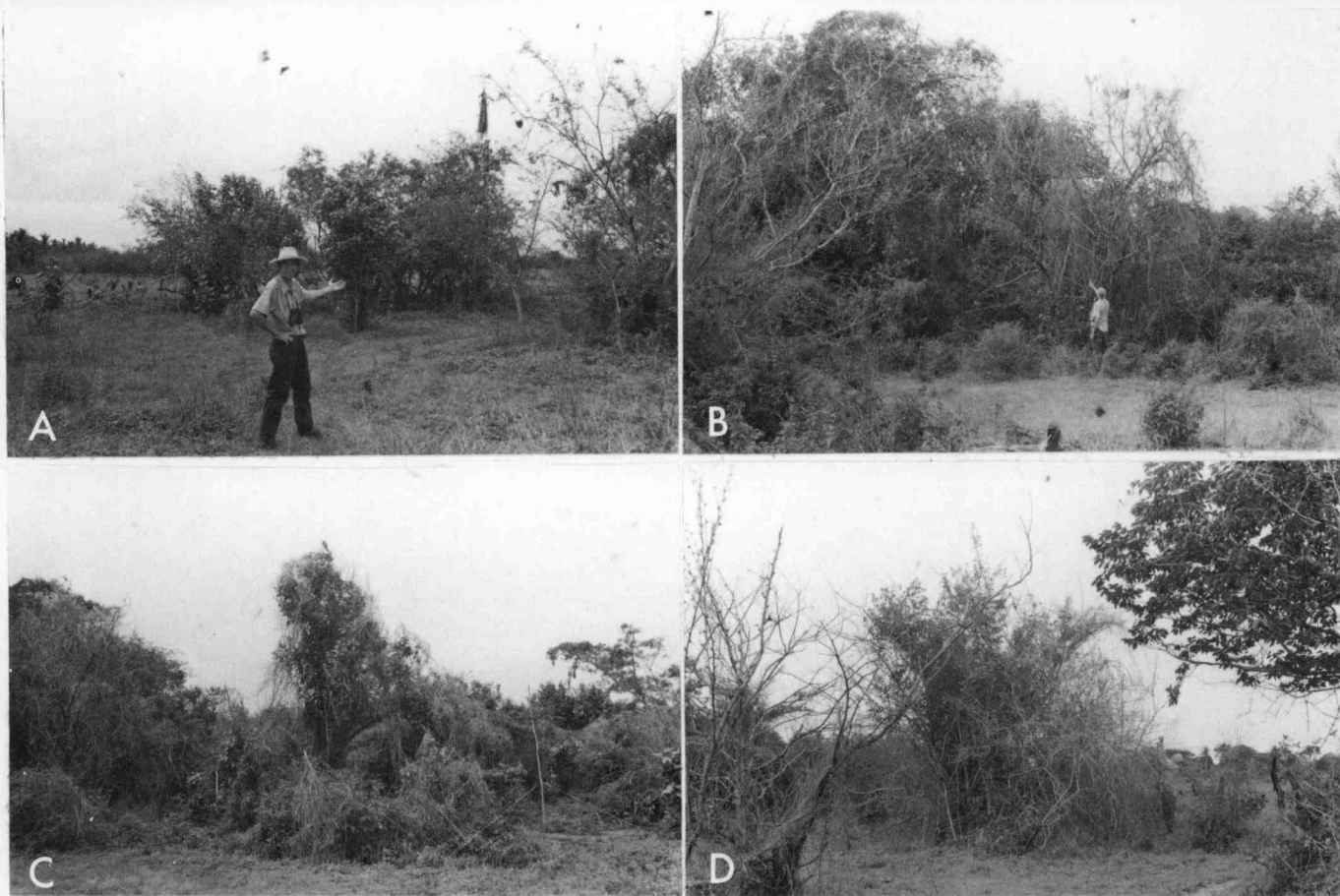|	1975	1976	1977	1978
Group 1				
Adults, 3 yr +	8	11	10	9
2 yr	3	1	2	2
1 yr	2	3	3	1
	13	15	15	12
Group 2				
Adults, 3 yr +		18	19	19
2 yr		1	3	2
1 yr		3	4	4
		22	26	25

FIGURE 4.   Patchy second-growth scrub woodland of the southern study site. (A) and (B) Men are indicating approximate locations of jay nests. (C) Thicket edge; the tallest middle tree held a jay nest. (D) Worker attaching a marker tag to indicate a jay nest tree.

were seen only once or twice each and their status was never determined). Groups 3 and 4 were never counted accurately. Our impression of group 3 was that it was slightly smaller than in the previous year. Group 4 had disappeared by 1977, as discussed previously under Nests and Principal Habitat. In 1978, group 1 had 13 members, and group 2 had 26 members. Other groups were not censused in 1978.

In most species of communally breeding birds, each communal group usually cares for only one or two nests (Brown 1978). The *Cissilopha* jays conform to this pattern (see Raitt and Hardy 1976 on Yucatan Jays, 1979 on Beechey Jays) with the exception of the Southern San Blas Jay. Groups 1 and 2 had from 6 to 10 active nests at one time. We were never able to count accurately the number of nests in groups 3, 4, and 5.

We found that most members of the Southern San Blas Jay groups were breeders, including some birds 1 and 2 years old. While it is not unusual in some other communal species for 1- and 2-year-olds to breed (Brown 1978), it is rare in the other *Cissilopha* jays.

NEST DISPERSION. — Table 3 shows that group 1 nests were in a single cluster and that group 2 nests were in two subclusters, with one linking nest (33) and two outlying ones (30, 38). Table 4 shows the sizes of the nest cluster areas and the percentage of the total home ranges that they comprised.

The nest clusters in the two groups in 1977 were of approximately equal density. Table 5 shows the mean distance from each nest to all other nests in its group that existed at the same time (not counting overlaps of up to 3 days). In group 1 the mean distance from each nest to all four neighbors was 117 m. To ascertain the comparable figure for group 2 we calculated the mean distance from each nest to its four nearest neighbors, which yielded a figure of 127 m.

We found no evidence that breeding pairs having one or more subadult members nested farther from their nearest neighbors (Table 5, nests 39, 33, and 38) than did older pairs.

The significance of nest cluster density and the placement of subadults' nests are considered in the Discussion.

THE ROLES OF HELPERS. — We found 10 nests being built. We were able to study construction at half of these; building was mostly by the female of the breeding pair, assisted or accompanied by her mate. In only one of these five cases was any bird other than the pair involved in any way: at nest 32 a female (Pi/Bl-R) accompanied the breeding pair for several days during nest building but did not add material to the nest. Other nearby birds apparently did not visit the nest in the construction stage.

We found no instance in which an incubating female (always the female breeder) was fed on the nest by any bird other than her mate.

TABLE 3.—Shortest distances between neighbor nests inside and outside their communal groups.

Distance from each nest to its nearest intragroup neighbor (m)[1]	Distance in meters	Nearest intergroup neighbors	Distance[2] in meters
Group 1, 1975			
N-3 – 5	44		
N-4 – 3	50		
N-5 – 3	44	N-4 – 6 (group 2)	135
N-9 – 5	72		
Group 1, 1976			
N-12 – 14	57		
N-13 – 12	64		
N-14 – 15	21	N-13 – 17 (group 2)	100
N-15 – 14	21		
N-16 – 14, 15, 20	100		
Group 1, 1977			
N-26 – 36	60		
N-27 – 36	120	N-27 – 28 (group 2)	160
N-34 – 39	85		
N-36 – 26	60		
N-39 – 26	75		
Group 2, 1975	(only three nests found)		
N-6 – 7	88		
N-7 – 6	88	N-6 – 4 (group 1)	135
N-8 – 6	95		
Group 2, 1976			
N-17 – 18	88		
N-18 – 17	88		
N-21 – 18	180	N-21 – 19 (group 3)	250
N-22 – 23	50		
N-23 – 22	50		
N-24 – 23	52		
Group 2, 1977	(only first nesting attempts included)		
N-28 – 29	50	N-28 – 27 (group 1)	160
N-29 – 28	50		
N-30 – 29	140	N-30 – 29 (group 3)	150
N-31 – 33	70		
N-32 – 40	65		
N-33 – 31	70		
N-35 – 31	80		
N-37 – 29	35		
N-38 – 32	150		

[1] Mean distance between nearest neighbor nests in group 1: 62 m, group 2, 80.3 m.
[2] This figure is given only for nests closest to borders of groups in which nests were known.

TABLE 4. — Sizes of home ranges and nest clusters (m^2) of communal groups of San Blas Jays.

Groups	Home Ranges	Nest Clusters	Nest Cluster/Home Range
1, 1976	90,500	20,500	22.6%
1, 1977	120,500	24,500	20.3%
2, 1976	130,749	13,049*	10.0%
2, 1977	250,000	68,000*	27.2%

*totals of 2 sub-clusters

TABLE 5. — Mean distance (m) from each nest to all other nests in its group.

		Group 1 Nests				
	26	27	34	36	39^2	$\overline{X}$
26[1]	-	160	160	60	75	113.0
27	160	-	125	120	120*[3]	135.0
34	160	125	-	170	85	135.0
36	60	120	170	-	90	110.0
39	75	120	85	90	-	92.5
						117.0

				Group 2 Nests						
	28	29	30	31	32	33	35	37	38	40	$\overline{X}$
28	-	50[4]	180	230	370	170	300	70	320*	410	117.5
29	50	-	140	200	320	140	260	30	280*	370	90.0
30	180	140	-	260	300	220	280	140	200*	360	170.0
31	230	200	260	-	170	70	80	170	210	200	122.5
32[1]	370	320	300	170	-	220	90	290	150	60	117.5
33[1]	170	140	220	70	220	-	140	110	240	260	115.0
35	300	260	280	80	90	140	-	230	170	120	108.0
37	70	30	140	140	290	110	230	-	250	340	87.5
38[1]	320*	280*	200*	200	150	240	170	250	-	180	175.0
40	410	370	360	360	60	260	120	340	180	-	155.0
											126.0

[1] Nests 26, 32, 33, and 38 each had one subadult breeder.
[2] Although technically this was a second nesting, see text p. 26 for account of unique circumstances that justify its inclusion here.
[3] Asterisked numbers were not used in calculating means because of nonsimultaneity.
[4] Underlined numbers designate four nearest simultaneous neighbors.

Helpers began to appear at the nest once the young hatched. Except for incubating or brooding females, most breeders were helpers simultaneously at one or more nests in their group, with some birds serving as attendants at all nests in their group having nestlings. Using only data from 1977, when we achieved the most complete record of nest attendance, we can see some manifestations of the communality of groups 1 and 2. In Figure 5 a line connects each two nests that had attendants in common, regardless of their identity or status. The number of lines as a fraction of the number of possible lines depicts the communal unity (C.U.) of the group. If a line has one arrow on it, the attendants were helpers first at the nest from which the arrow originates and then later at the nest to which the arrow is directed. Similarly, two arrows on a line indicate reciprocity in this regard. The fraction of reciprocities recorded of the total number possible (given a biological "need" in the form of nestlings requiring feeding) is a communality index (C.I.). The C.I. of 0.83 (5 of 6 lines between nests that produced nestlings having two arrows) for group 1 in 1977 was about as high as it could be, because nest 39 failed prior to hatching and nest 34 failed when the nestlings still required little food. The subdivided nature of the group 2 nest clusters seems to account for that group's lower C.I., which at 0.29 (9 of 31 lines double-arrowed) is still indicative of communality. Initial study of this group suggested that it might not be unified in that no network of attendants seemed to connect the subgroup nest clusters. Long-term study revealed that while the frequency of appearance of birds at each other's nests was low when nests were far apart, such attendance did occur, as the lines and arrows show. A line and one arrow need be based upon only a single feeding visit from a bird primarily associated with another nest, and it might be argued that this is slim evidence for communality. This record of social relationship becomes more impressive, however, when one realizes that in the five seasons of study, the inter-nest-cluster C.I. and C.U. were zero.

A comparison of the roles of parents and nonparents (pure helpers) in maintaining unity and communality shows little difference between the two (Figs. 5 and 6). Male breeders had relatively little to do at their own nests while their mates laid and incubated, and spent some of this time helping at neighboring nests. Thus most social connections by breeders were maintained by the males. Breeding females were helpers prior to egglaying, or after their young were fledged or their nests abandoned. The C.U. of group 1, based only on parental contacts, was 0.80 (8 of 10), the same as with pure helper representation. The C.I. of only 0.17 (1 of 6) is expectable when one considers the roles of breeding vs. nonbreeding attendants: the earlier-nesting, successful parents may be wholly involved with fledged young and have less time to reciprocate by visiting later nests to feed nestlings. Some helpers may have involvement with earlier broods
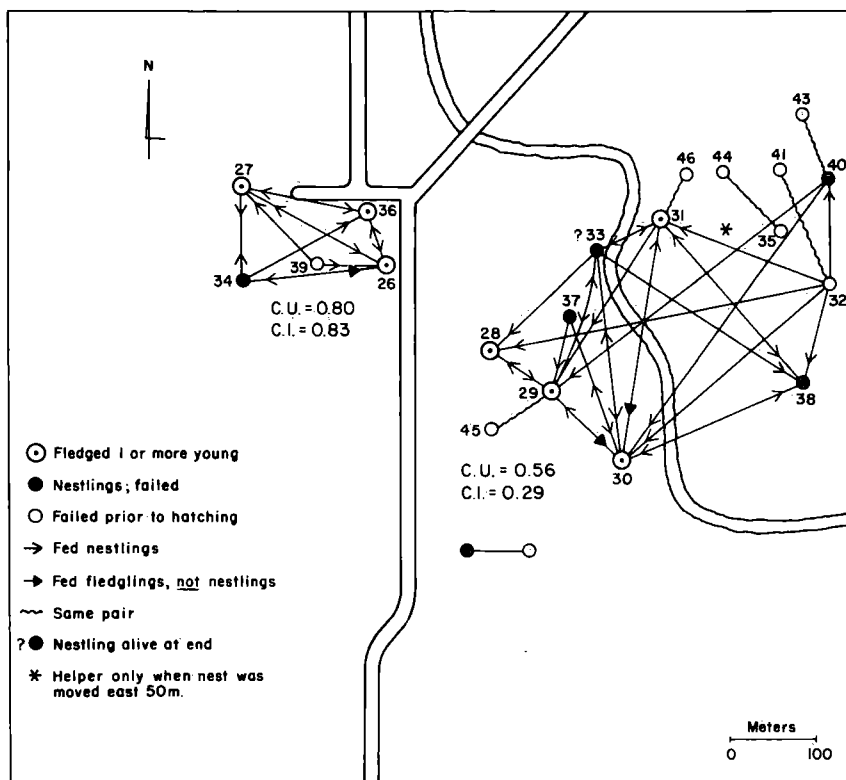
FIGURE 5. Communal contacts of groups 1 and 2 based on all nestling or fledgling attendants in 1977. Numbers near circles are nest number designations. See text, page 15 for definition of C.U. and C.I. and discussion and explanation of arrow directions.

as well, but not to the same degree. Group 2 had only 12 of 36 possible social connections by parents only, for a C.U. of 0.33 and 3 of 9 (0.33) social connections were reciprocal. Apparently this lower C.U. was caused by two factors: the long distances between many nests and the greater number of nests having virtually identical timing. Birds feeding their own nestlings seldom visited other nests. Breeders of nests 33 and 37 were prominent assistants at nest 29 while building their own nests. The male breeder of nest 40 attended at nest 29 after nest 40 was abandoned. Breeders at nests 32 and 41 became helpers at nest 38 after both their attempts failed.

TEMPORAL PATTERNS OF NEST ATTENDANCE AND SOCIAL STATUS OF NEST ATTENDANTS. — In Southern San Blas Jays at least five factors interact to produce a complex sociality: (1) the groups are unusually large for a communal species, (2) the number of breeding pairs per group is high, (3) the timing of the various nests within a group is staggered (Figs. 7 and 8), (4)

most birds are both parents and helpers, and (5) successful early nests reduce attendance at later nests and perhaps their success.

Early nests were virtually certain to attract assistance from non-breeding helpers and from late breeders who were just starting to select nest sites or to build. Later nests often had few or no helpers: parents that nested earlier were renesting if they failed or attending their own fledglings if they succeeded.

Nonbreeding helpers also tended to move around with the juveniles and not visit later nests. Figures 9 and 10 illustrate the above points. These figures as well as Figures 11 and 12 are constructed from observation periods that were virtually or completely uninterrupted, contained few or no questionable identifications of individual birds, and represented, when possible, days throughout the nesting period or a sequence of days in the week before fledging. With two exceptions, the
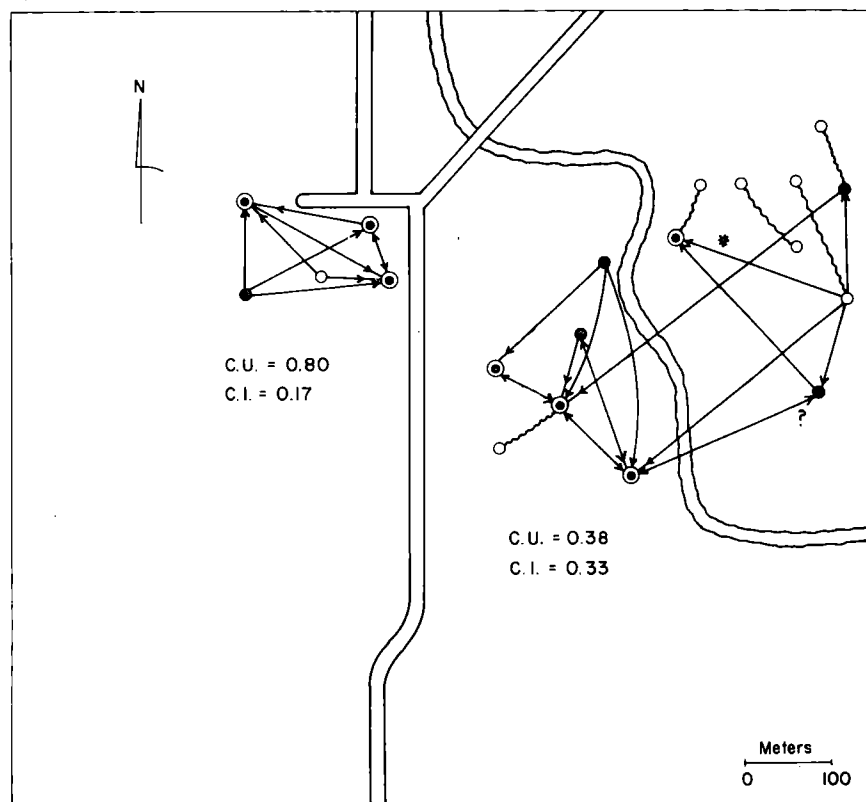
FIGURE 6. Communal contacts of groups 1 and 2, 1977, based only on attendants that were breeders in the same season. See page 15 for definition and discussion of C.U. and C.I. See Fig. 11 for other symbols.

GROUP 1
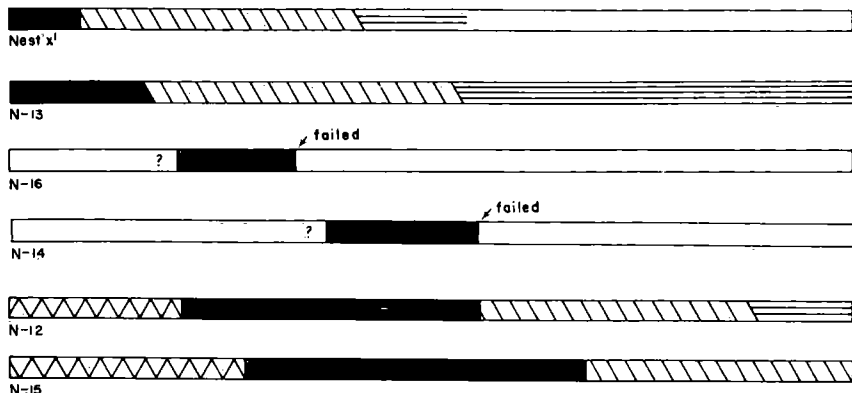
FIGURE 7. Timing of stages in the development of nests in groups 1 and 2 at the main study site, 1976. Note staggered timing of nests in both groups.

periods selected were an hour or more long. Some birds recorded as helpers in Appendices I and II did not happen to visit a nest during the observation periods represented in Figures 9-12, hence the discrepancy between the figures and appendices.

In 1977, nest 27 was the first active nest in group 1. The many attendants included yearling nonbreeders such as BlBl and Pi/Bl-L, as well as all male parents at later nests: OPi, OBl, PiG, and PP. The young from nest 27 fledged on 18 June, though only one survived the first few days. Nest 26 (Fig. 9) was the second to fledge young, on 4 July. Therefore, nest 26 also had a sizeable group of attendants, although note that
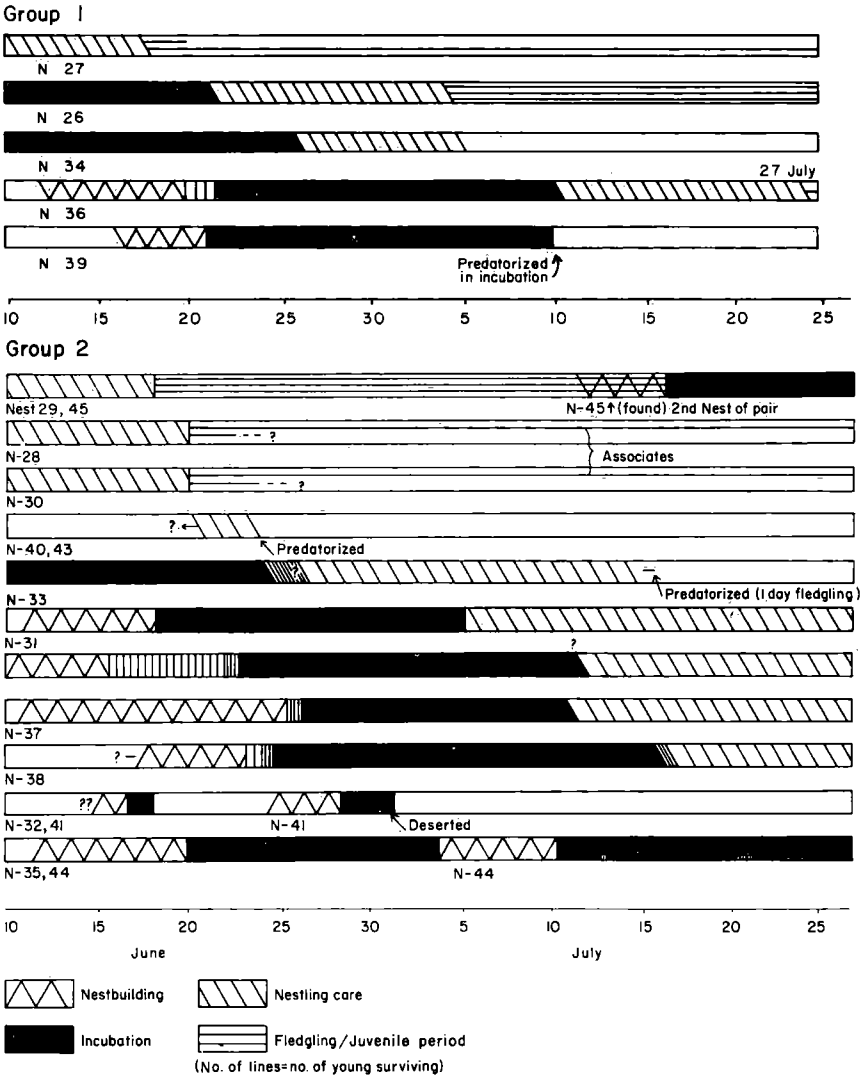
Group 1

Group 2

FIGURE 8.   Timing of stages in the development of nests of groups 1 and 2 at the main study site, 1977. Note staggering of nests in group 1 but near-simultaneity of some nests in group 2.

compared to the small parental contribution to feeding at nest 27, nest 26's nucleus pair contributed roughly half the feeding visits per hour. Nest 26 fledged three young and simultaneously we introduced three orphan fledglings from outside the study area. Unfortunately for the comparison of the number of helpers at all nests of group 1 in 1977, nest 34 (Fig. 10A) failed after about one week of nestling life, too early to allow
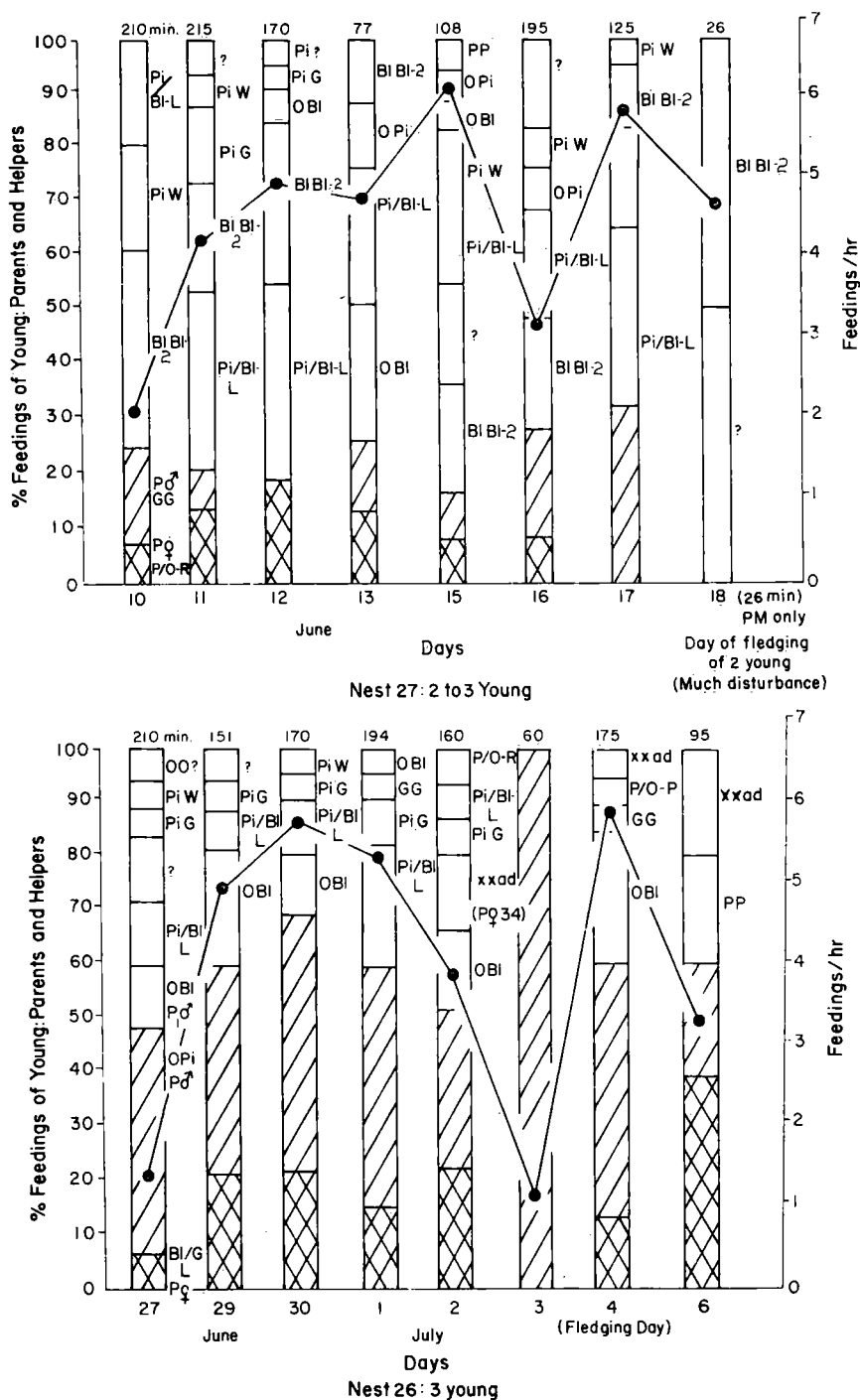
FIGURE 9.   Percentage contribution of attendants and rates of feeding visits at nests 27 and 26, 1977. Note a larger number of attendants at both nests but higher contribution of parents at nest 26.

FIGURE 10.   Percentage contribution of attendants and rates of feeding visits at nests 34 and 36, 1977. Note low feeding rate at nest 36 with only one young, and compare to the rate at nest 37 (Fig. 12) with the same number of attendants, but with three nestlings.

examination of the helper's contributions. Nest 36 (Fig. 10B), however, clearly shows the effects of the existence of seven juveniles needing care in group 1. Note that virtually all attendance was by the breeding pair. We saw only three contributions by others. Of these, only PiW actually fed the young; in the other two feedings, food was delivered to the female breeder who gave it to the young. One of the two nestlings fledged at nest 36.

In group 2, 1977, nests 28, 29, and 30 show variations on the above-described theme (Fig. 11). In the western part of the group's range, these three nests were almost simultaneous in development, nest 29 fledging its young on 18 June, the other two on 20 June. At nest 28, the only regular attendant other than the breeding pair was WBk, their offspring of the previous year. In the observation periods shown in Figure 11, BlW may have fed once (identification not certain); outside these periods the breeding pair of nest 29 (OW, XX ad.) and the female breeder of nest 33 (BlPi) were definitely recorded as feeding once each at this nest. It seems as though nest 29, in operation at the same time as nest 28, attracted more helpers because of its central position (see Fig. 2). Nest 29 drew regular attendance from the breeders of nests 33 and 37, both of which were under construction. Less help came from WO, WBl, WBk (nest 28), the breeders at nest 30, Bl/G-R, a 2-year-old, and the helper Pi/G-R at nest 31. Figure 11 of nest 30 suggests that it suffered similarly from isolated position and the concentration of helpers at nest 29, but the data are too few for this to be certain. Ten birds were seen to attend the young of nest 30. The parents were the principal caretakers at this nest, assisted mainly by the 2-year-old Bl/G-R. Others were seen to visit only once each. The virtual absence of helpers at nest 36 in group 1 and nest 37 in group 2 seemed in both cases to be due to the nearby presence of fledglings. By the time the nestlings of nest 37 (Fig. 12) were ready for helpers, nest 28 had fledged three young, nest 28 had fledged two, and nest 30 had fledged one (Fig. 11). Of these young, five survived and were being cared for by parents and helpers of nests 28, 29, and 30. Figure 12 shows that in the long watch periods at nest 37 only the two parents, OBk and Pi/O-R, attended the nestlings. (Otherwise, only P/G-R, the female breeder of nest 30, was seen to visit that nest.)

VARIATION IN THE RATE OF NEST ATTENDANCE. — Table 6 summarizes data on the frequency of feeding visits, number of attendants, and rates of feeding visits per nestling. Total observation time and days spanned by observations varied considerably. From Table 6 we have used the seven nests (numbers 12, 22, 26, 27, 28, 29, and 30) with the best data on care of nestlings, either throughout their nest life or in the latter part of that period when helpers are prevalent, to examine relationships between brood size, feeding rates, and number of attendants. Spearman correla-

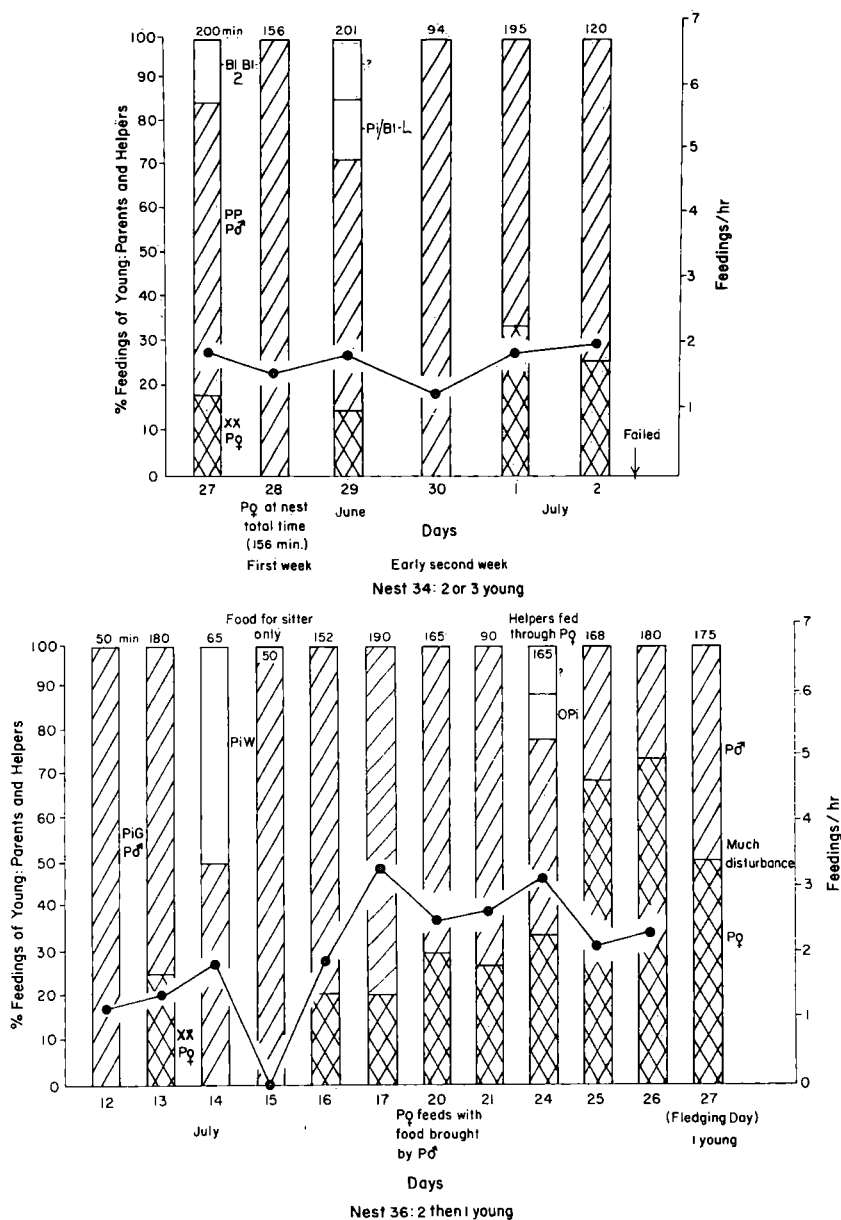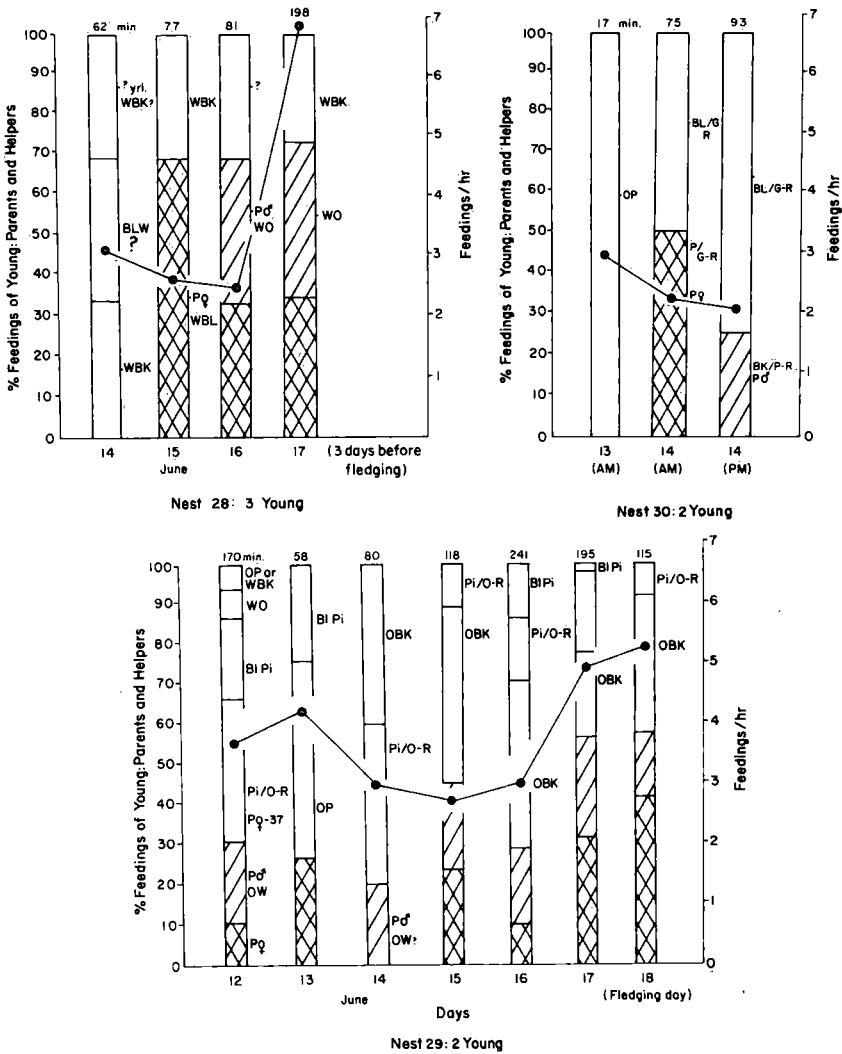FIGURE 11.   Percentage contribution of attendants and rates of feeding visits at nests 28, 29, and 30, 1977. Note that of these three simultaneous nests in close proximity to one another, only one had a large and persistent complement of helpers, and most of these were breeders.

tion coefficient tests yielded the following results: a highly significant negative correlation between number of frequent attendants and feeding rate per frequent attendant ($r_s = -0.906$, $P < 0.01$), and a significant positive correlation between brood size and total feeding rate ($r_s = 0.798$, $P < 0.05$). The correlation between feeding rate per frequent attendant and feeding rate per nestling is just below significance at the 0.05 level
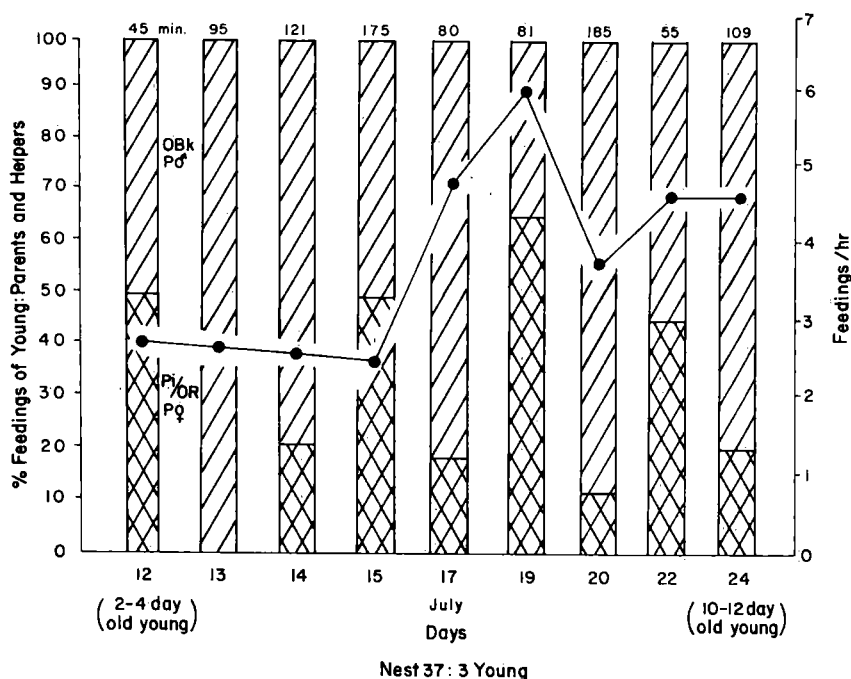
FIGURE 12.   Percentage contribution of attendants and rates of feeding visits at nest 37. Compare high rate of feeding of the three nestlings with lower rate at nest 36 (Fig. 10) by the same number of attendants.

$(r_s = -0.746)$. There is a suggestion of a correlation between number of frequent attendants and feeding rate per nestling, but it is not statistically significant $(r_s = 0.717, P > 0.05)$. The feeding rate per nestling did not increase with brood size $(r_s = -0.16, P > 0.05)$. The feeding rate per nest is not correlated with number of frequent attendants $(r_s = 0.321)$. The brood size is not correlated with the number of frequent attendants $(r_s = -0.083)$. In summary, the amount of food received by nestlings and the work of bringing it by attendants form a complex relationship in which the availability of more attendants reduces the work load of individual attendants, and the number of feeding visits required to serve the young is directly related to the size of the brood. Still, nests attended only by parents and a few helpers apparently received just as many feeding visits as those with many attendants.

We do not have enough data to provide information on the relationship between the number of attendants and nesting success.

KINSHIP AS A FACTOR IN ATTENDANCE. — We were able to follow only six birds of known parentage from fledging through to their roles as attendants at nests. All these birds helped their parents if their parents had

TABLE 6.—Summary of nest attendance data for San Blas Jays, groups 1 and 2, 1976, 1977.

Group, Year	Nest	Brood Size	Frequent Attendants (Total No.)	Total Obs. Time in Hrs.	Span of Obs.	Rate of Feeding	Rate/Nesting[1]	Rate/Frequent Attendant
1 1976	12	2	4(7)	16.8	9-21 July Last 11 days of nestling period	3.4/hr.	1.7	0.85
	13	3	5(11)	4.3	3 days, beginning of last week of nestling period	4.4/hr	1.5	0.88
	15	2	2(7)	7.45	18-22 July	2.7/hr.	1.35	1.35
2 1976	18	2	?(8)	-	-	-	-	-
	21	2	2(7)	1.8	4 July	5.3/hr	2.65	-
	23	3	(12)	-	-	-	-	-
1 1977	22	2	3 or 4(8?)	6.5	Last 7 days	2.9	1.45	0.97
	27	2	7(8)	27.35	Last 9 days	3.7/hr.	1.85	0.53
	26	3	5(11)	26.05	Entire	4.4/hr.	1.47	0.88
	34	2-3	2(4)	16.90	First week (Destroyed)	1.7/hr.	-	-
	36	2-3(early) 1, mid-late	2(7)	27.20	Entire	1.8/hr.	1.80	0.9
2 1977	28	3	3(7?)	11.1	Final week	4.5/hr.	1.50	1.50
	29	2	5(14)	22.73	Final week	3.2/hr.	1.60	0.64
	30	2	3(10)	3.08	Final week	2.9/hr.	1.45	0.97
	31	2	3(7)	6.70	First week	1.04/hr.	0.52	-
	33	? > 1	3(4)	9.50	First 11 days	2.0/hr.		-
	37	3	2(3)	17.30	First 2 weeks (almost entire)	3.5/hr.	1.17	1.75
	38	? > 1	2(6?)	14.5	From 13th to 15th day	2.4/hr.	-	1.20
	40	? > 1	2(3)	3.9 / 223.16	2 days at end of ca first week	1.02/hr.	-	-

[1] Where data are not supplied in the last two columns, it is because they were too few or from early in the nesting period and thus do not reflect accurately the rates of attendance.

young to feed, although help was delivered to the first nest that produced young, regardless of the identity of the breeders there.

OBl was an offspring of OPi and PiO in 1975. In 1976 he was known to have been a helper at three nests, the first that of OPi, his father, and Bl/G, his stepmother, PiO his mother having disappeared. In 1977, as a 2-year-old, OBl was paired to BlBk at nest 26. That nest and its eggs were taken over by OBl's father OPi and OPi's mate, Bl/G-L. OBl then was mate, Bl/G-L (G/O-L having been killed by a predator). OBl then was recorded as a helper at nest 26, thus being a helper to his own young for his father, the grandfather of the young! In 1978, OBl was apparently breeding with BlBk again, although the nest was not found.

WBk was the sole offspring of WO and WBl at nest 18 in 1976. In 1977 he was a nonbreeding helper at his parents' nest (28) and rarely at nearby nest 29. WBk was apparently still a helper at his parents' nest in 1978, but the young had fledged before we arrived.

Pi/G-R was an offspring of OP and Pi/Bl-R at nest 22 in 1976. Pi/G-R helped at three nests in 1977. It helped first at nest 31, which produced young early in the breeding season. Later it helped at nest 33, its father's nest, and at nest 38, both of which had nestlings of about the same age.

All three offspring of BlO and O/G-L at nest 13 in 1976, BlBl-2, Pi/Bl-L, and PiPi-2, were helpers in group 1 in 1977. Nest 27, owned by GG and P/O-R, was the first nest known to have nestlings in group 1 in 1977. All three sibling yearlings helped there. BlBl-2 and Pi/Bl-L were also active helpers at nest 26 (owned by OPi), the second nest in the group to produce nestlings. Thus at nest 26 they were feeding nestlings, which, though in a nest "owned" by OPi were actually the offspring of OBl. BlBl-2 and Pi/Bl-L were also active feeders of the fledglings of nests 26 and 27 and the orphans we introduced. In 1978, only Pi/Bl-L of the three sibs remained in group 1 and was seen as a helper with the putative fledglings of OPi and Bl/G-L. Some young, such as WBk, may even show some nearly exclusive attachment to their parents, but nearby nests with earlier young usually attracted attendance by such birds.
birds.

AGE AT FIRST BREEDING. — Of seven jays marked as either fledglings or yearlings and followed at least to their first nesting attempts (see Appendix I), two males PiG and OBl, and one female, BlPi, attempted to nest as 2-year-olds; three, PP and Bl/G-R, both males, and BlW, a female, nested first as 3-year-olds. GG, a male, nested first as a 4-year-old. Of all 14 yearlings whose activities were well known, only 2 (both females) attempted to nest; of all 10 well-known 2-year-olds, only 4 (3 males, 1 female) attempted to nest. We conclude that although most individuals first attempt to breed in their third year, and rarely the fourth, attempts by yearlings and 2-year-olds to breed were of regular occurrence in the

groups studied. The possible significance of breeding by subadult birds (less than 3 years old) is treated in the Discussion.

BREEDING TIME OF ADULTS VS. SUBADULTS. — Nests involving subadults as breeders were usually late, among the last to be initiated in the communal groups studied (Fig. 13). The one exception was nest 26 in group 1, at which OBl was the 2-year-old male breeder. This nest was second only to nest 27 in the temporal sequence. It may be significant that OBl matured early in plumage and softpart color, being without crest feathers and having yellow irides only faintly tinted with green in the second year. Because we terminated study each year before the fate of late nests could be known with certainty, we lack data on the relative success of late and early breeding attempts.
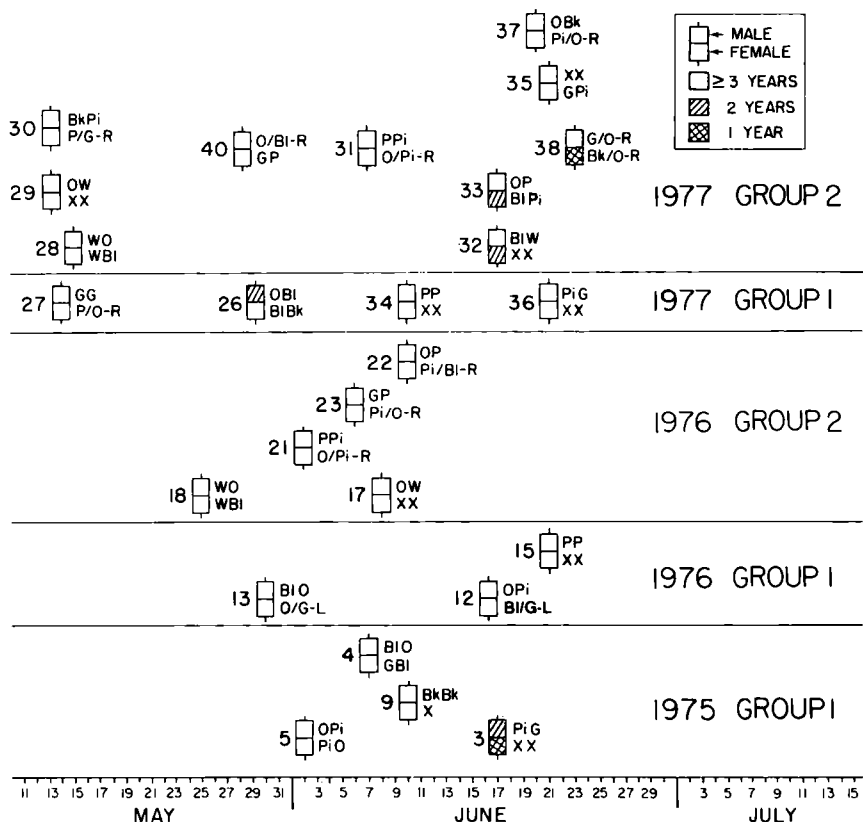

FIGURE 13.   Approximate dates of egg-laying for three age classes of breeders in first breeding attempts of the season. Pairs in which yearlings or 2-year-olds are members tend to nest later.

PAIR BOND PERSISTENCE

In 17 cases both members of the pair survived from one year to the next. (Three of these cases involved unmarked adults: OW's mate from 1976 through 1978 and PP's mate from 1976 through 1977 were unmarked.) In only one known case were the birds not mated to each other in the second year. OP's 1976 mate, Pi/Bl-R, was seen briefly in June 1977 and then disappeared. The bird may have been sick and was associating with another pair (XX, a 2-year-old, and BlW) that was building nest 32. However, OP already had another mate, BlPi, at this time. We conclude that these jays normally mate for life or until one leaves the communal group.

HOME RANGE

Figures 14 and 15 show the almost exclusive home ranges (as well as nest locations) of San Blas Jay communal groups in 1976 and 1977. These home ranges were maintained by mutual avoidance rather than by active defense. On many occasions birds of neighboring groups came close to each other at boundaries between ranges, sometimes into the same trees, without any signs of intergroup hostility. We noted no vocalizations or postural displays specialized for territory defense. On the rare occasions when trespassing occurred the intruder moved swiftly and inconspicuously and avoided confrontation with residents. In 1975, group 2 birds, such as OW and WO, occasionally flew at palm-crown height with at most one stop across the nest area of group 1 to the west jungle patch (Fig. 1). This behavior apparently stopped in 1976 after the west jungle patch was largely cut down. An adult stranger netted in the heart of group 1's range in June 1975 and never found there again was finally found to be a member of group 5 from 1975 through 1977.

INTRAGROUP CORE AREAS

Within communal group 2 we regularly saw strong evidence that breeding pairs verged on territoriality toward members of their own group. Especially when their nests had contents, male breeders restricted their movements to small "core areas" around their nests and exerted various degrees of dominance over intruders. Figure 16 shows the core areas of males G/O-R, OP, XX ad, and OBk in 1977.

Group 1 rarely showed such intragroup hostility, probably because of its small size, smaller home range, and the resulting greater familiarity among its members.

Male breeders of group 2 restricted their visits away from their core areas almost exclusively to gathering food hastily and returning as soon as possible. When inside their core areas, they typically made short flights
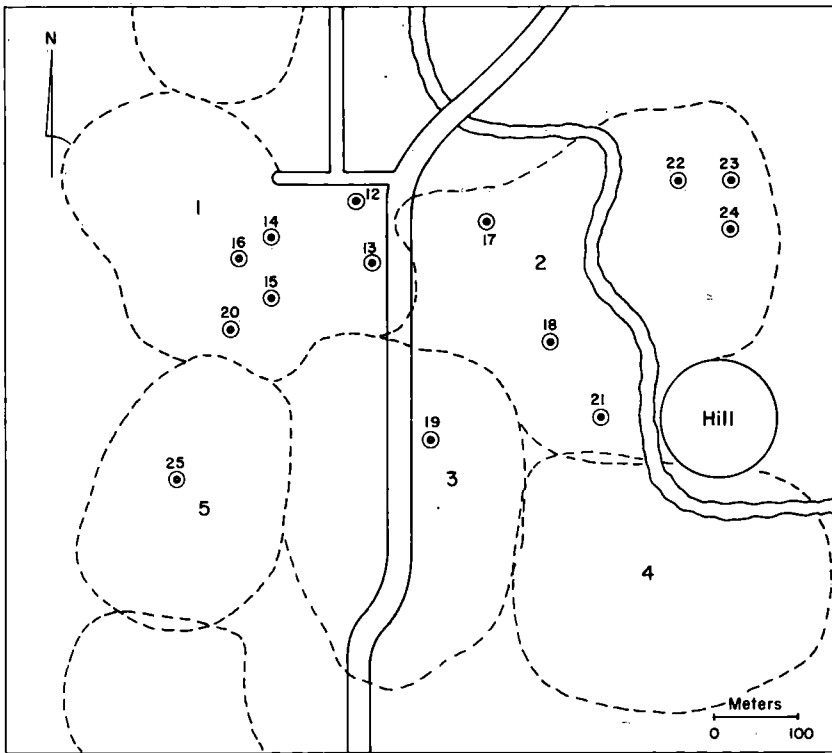
FIGURE 14. Distribution of known nests and group home ranges at the main study site, 1976. for communal groups 1-5.

interrupted by long pauses, but when venturing outside, they made long uninterrupted flights to the objective and spent relatively little time there (Table 7). Of 72 recorded pauses in his core area, G/O-R preened in 7, did sentry duty in 24, foraged in 32, and scolded in 19. In his 10 visits to the central mango out of his core area, G/O-R only gathered food. Once while birds of the nest 33 subgroup were mobbing the observer at the mango tree because their fledgling was nearby, G/O-R fed in the same tree but took no part in the mobbing. Moments later G/O-R retreated to his core area and at its boundary immediately began to scold the observer. Of the 71 recorded pauses of OP in his core area, he preened in 3, did sentry duty in 13, foraged in 63, and scolded in 6. Outside his core area, OP was never seen to perform any of these behaviors except foraging.

Birds other than the breeding pair rarely entered the core area when the residents' nest held eggs. After the young were about one week or more old, the traffic of nonbreeding helpers became more frequent and
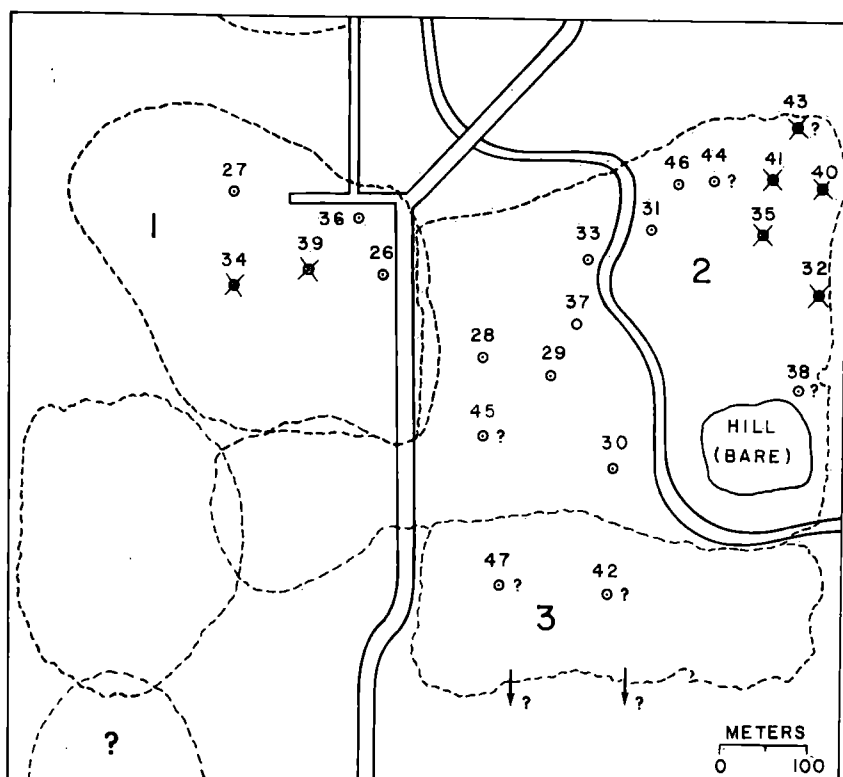
FIGURE 15. Distribution of known nests and home ranges at the main study site for communal groups 1-3, 1977. Note that group 4 no longer existed, that group 2 had usurped part of group 3's range, and that group 3 had extended into part of group 4's range.

the sudden appearance of less frequent helpers, including other breeders, was noted more often. Within his core area, each male breeder confronted all pausing strangers by approaching, perching near them, peering at them intently, and sometimes supplanting them. Intruders typically remained quite still at first. Sometimes the action was broken off by the retreat of the stranger, chased briefly by the resident male, but if the intruder remained, the male approached closely, the stranger begged, gaping and fluttering its wings, and the male appeared to feed it. On occasion actual feeding occurred if the male happened to have food in its bill; but as often as not the male merely poked its bill into or at the stranger's gape. Sometimes the intruder itself already had a mouthful of food, further emphasizing the ritualistic nature of the act. On rare occasions the intruder would Upfluff when confronted by the resident, and in response the resident would Peck-preen it, as described by Hardy (1974).

As in the captive jays Hardy (1974) studied, the full ritual display of
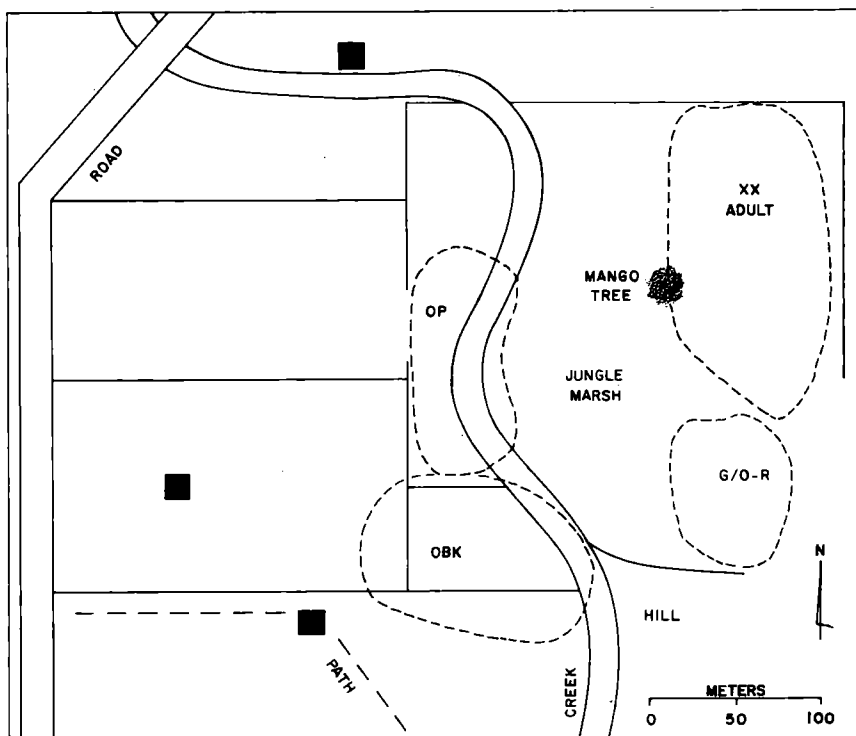
FIGURE 16.   Core areas of 4 males in group 2, 1977.

begging and feeding was seldom seen between individuals that were in daily contact with each other. In the captives one could stimulate the full display by introducing strangers or removing a familiar bird from the group for a few days to a week, and then reintroducing it. Upfluffing and Peck-preening were seen daily in captives, because confinement probably led to an increased frequency of encounters, but were seen far less often in wild birds.

In the wild, *regular* visitors, usually yearling or 2-year-old helpers, were not treated in this ritualistic way. Relative strangers that persisted in visiting were soon ignored as well. For example, BlW and XX 2-year-old failed in two nesting attempts in 1977 (nests 32,41). A few days after their second nest failed, they began to visit the core areas around nests 40 and 38. In these initial visits they begged to and were fed by the resident male breeders. A few days later it became clear that XX 2-year-old and BlW had foregone further nesting attempts and had "adopted" nest 38, for their visits had increased to several per hour. Not only were they allowed to enter the core area and visit the nest unconfronted by G/O-R, but their attention to the nest became so regular that they could easily have been

TABLE 7.—Movement of two male San Blas Jays inside and outside their core areas.

Bird	Distances Flown (m)		Duration of Pauses (min.)	
	$\overline{X}$ out	X in	$\overline{X}$ out	$\overline{X}$ in
G/O-R	74 (N = 17)	26 (N = 72)[a]	2.4 (N = 10)	7.2 (N = 85)[c]
OP	86 (N = 14)	9 (N = 75)[b]	——	——

[a]one-tailed Mann-Whitney U test; t_s = 5.21; P < 0.001
[b]one-tailed Mann-Whitney U test; t_s = 6.29; P < 0.001
[c]one-tailed Mann-Whitney U test; t_s = 2.83; P < 0.005

mistaken for the breeding pair. Once when P/G-R, the female breeder of nest 30, paid a rare visit to the nest 38 tree, XX 2-year-old confronted her, stared at her intently, and she left. Thus the male helper behaved like an owner in the absence of the actual male breeder, G/O-R.

The changing nature of interactions between birds reflected changes in their nesting status. For example O/Pi-R, the male breeder of nest 31, often confronted visitors to the mango tree at his core area border with ritualized dominance behavior. In a 2-day period when the nestling in nest 31 was fledging and then was killed, O/Pi-R was first dominant toward one neighbor, XX ad. male, and in the same area the following day performed appeasement begging toward another, G/O-R. Apparently its tendency toward dominance in this part of its core area waned with the loss of the fledgling. Not only did the dominant nature of the resident male wane when the nesting was interrupted, but he also resumed wandering much more widely over the group's home range, sometimes alone and sometimes with his mate, seemingly in search of a new nest site. When the pair of nest 31 renested farther northwest, the male's core area boundaries shifted accordingly.

On rare occasions the behavioral roles of the confrontees were switched. On three occasions we saw the patrolling male resident beg from the intruder. In one of these cases, the roles then abruptly switched, with the intruder begging to the resident. In the other two only the intruder performed the feeding ritual. In these two cases, both involving the same two males, we were sufficiently familiar with the circumstances and individuals involved to offer the following explanation. Older birds generally dominate younger ones (Hardy 1974). We judge that this dominance prevailed in the reversed roles. OPi, the breeding male at nest 26, was at least 5 years old when the interaction occurred in 1977. PiG, a 4-year-old, commenced building nest 36 when OPi and his mate Bl/G-L had large nestlings. Nest 36 was well within the frequent foraging area of, and perhaps in an area dominated by, OPi and his mate. As mentioned previously, nest 36 young were being cared for almost completely by the parents when OPi's young were nearly full-grown juveniles. So few of the

otherwise occupied group 1 members ever approached nest 36 that all could be considered virtual strangers in that area and thus not freely allowed at the nest. On one of the rare occasions that one of the birds (OPi) caring for fledglings in the group's range approached nest 36 with food, the food and OPi's probably dominant relationship to PiG triggered the begging response in the latter, who accepted the food and took it to the nestlings.

NATALITY AND MORTALITY

OVERALL NESTING SUCCESS. — Of accessible nests in the main study area with apparently complete clutches, four had four eggs and three had three. Most nests could not be examined safely or accurately because of their height, protective placement, or both. For the purposes of Table 8 and the following discussion of mortality, clutch size is assumed to be 3.6 eggs. Although 50-67 % of the nestings that had clutches produced at least one fledgling, only 22-38 % of eggs resulted in fledglings (see Table 8, columns 4 and 5).

BREEDING SUCCESS OF SUBADULTS VS ADULTS. — Fully adult birds were more successful breeders than 1- or 2-year-olds. Twenty-six nestings, the results of which were known or strongly suspected, were used to compare nesting success of adults and subadults. Nesting attempts in which both parents were adults (nests 4, 5, 9, 12, 13, 15, 26, 27, 34, 36 of group 1 and 17, 18, 21, 22, 23, 28, 29, 30, 31, 35, 40 of group 2) succeeded in fledging at least one young in 15 of 21 cases and a total of 30 young, almost two young per nest. All four nests involving at least one subadult pair member were unsuccessful. Of these nests, one involved a 2-year-old male and a yearling female, and three involved a 2-year-old male and an

TABLE 8. — Nest success in San Blas Jay Groups 1 and 2.

Groups and years	No. of nests of known fate	No. of these nests producing nestlings (%)	No. of these nests producing at least one fledgling (% nests producing fledg.)[1]	No. fledg. per total eggs [2] (%)
Group 1				
1975	5	5 (100)	3 (60)	4/18 (22)
1976	6	4 (67)	3 (50)	8/21 (38)
1977	5	4 (80)	3 (60)	6/18 (34)
Group 2				
1976	6	5 (83)	4 (67)	8/22 (38)
1977	8	5 (62)	4 (50)	8/29 (29)
Totals	30	23 (77)	17 (57)	34/108 (31)

[1]Fledglings/nests = 17/30 (0.56/nest).
[2]Based on all nests in column 2 and a 3.6 mean clutch size.

adult female. Nests 33 and 38, the fates of which were not discovered, involved adult males and 2-year-old and yearling females, respectively. Both had mid-stage nestlings at the termination of study in 1977. Comparative numbers are disparate, as pairs involving subadults are in the distinct minority, but a chi-square test confirmed that the proportion of successful breeders was significantly greater in adult × adult pairs than among others ($X^2 = 7.15$, d.f. = 1, $P < 0.01$).

CAUSES OF NESTLING LOSS. — The causes of nestling mortality were difficult to detect. We saw Great-tailed Grackles *(Quiscalus mexicanus)* and Groove-billed Anis *(Crotophaga sulcirostris)* around jay nests, and saw jays attack both species there. These seem the most likely avian predators on nest contents, but we saw no such predation. Skutch (1958) mentioned this grackle as a possible predator on eggs of a small tanager *(Euphonia lauta)*, and Lamb (1944) saw a Great-tailed Grackle seize in its bill and kill a Yellow Warbler *(Dendroica petechia)* as she tried to defend her nest against it. Wetmore (1927) recorded the Smooth-billed Ani *(C. ani)* as an egg predator of the Greater Antillean Grackle *(Holoquiscalus niger)* in Puerto Rico. Olivares and Munves (1973) reported Smooth-billed Ani predation on nestlings of Vermilion Flycatchers *(Pyrocephalus rubinus)* in Colombia. In groves the jay used for nesting, squirrels were too rare to constitute an important hazard. Snakes seemed uncommon. We noted one unidentified small snake try unsuccessfully to climb a palm trunk. We saw no snakes among the palm fronds. Although iguana lizards *(Iguana iguana)* live in the native woods and we saw a dead one on the road through the coconut groves, we did not see any in the palms. Heavy storms can blow down palm fronds or coconut clusters and the nests supported by them. In 1975 one nest was blown down in the late nestling stage, killing the single nestling it contained. Clearly in years of much stormy weather in July, weather can be an important cause of mortality, although such weather failed to materialize in 1976 and 1977. The major cause of prefledging mortality during our study may have been predation by grackles and anis. Another possible cause is human disturbance. Each grove was occasionally harvested of coconuts, and nests resting on coconut clusters came down with the harvest, but no nest failures noted in our prefledging figures (Table 8) could be attributed to such disturbance. Nest 31 and its two nestlings were knocked down, but we replaced it in a low tree near by and the attendants resumed care of the young. Nest 22 nestlings were force-fledged perhaps 2-3 days prematurely when their nest was knocked down by coconut harvesters, but survived the fall and were not abandoned.

POST-FLEDGING SURVIVAL AND MORTALITY. — Appendix III and Table 9 show that the annual survival rate of birds after their first year was never below 57% and generally ranged above 75%. In contrast, of 19 flagged

TABLE 9.—Annual survival, based on marked birds only of Southern San Blas Jay groups 1 and 2.

	Adults (3 yrs. +) % (N)	1- and 2-year-olds % (N)	Fledglings % (N)	Over-all total % (N)
Group 1				
1974-5	60 (3/5)	100 (3/3)	25 (1/4)	58 (7/12)
1975-6[1]	57 (4/7)	60 (3/5)	50 (1/2)	57 (8/14)
1976-7	80 (8/10)	50 (2/4)	43 (3/7)	62 (13/21)
1977-8	78 (7/9)	60 (3/5)	0 (0/6)	50 (10/20)
Group 2				
1974-5	—	—	—	—
1975-6	100 (8/8)	67 (2/3)	0 (0/2)	77 (10/13)
1976-7	81 (13/16)	75 (3/4)	25 (2/8)	64 (18/28)
1977-8	88 (15/17)	67 (4/6)	0 (0/8)	61 (19/31)

[1]Does not consider PiBk, which immigrated to group 1 in 1976.

fledglings in group 1, only 5 (26%) were present on the study area one year after hatching, while in group 2, 2 (11%) of 18 were present. Nor were any of those missing found elsewhere.

In group 1 we banded 39 birds of all ages. Of these, 19 (49%) survived to at least the next breeding season. Of the 39, 19 birds were banded at yearling age or over, of which 13 (68%) lived at least to the following year. Of the 13 banded as adults, 9 (69%) survived at least one year.

We banded a total of 43 birds in group 2. Of 25 (58% of the total) banded as yearlings or older, 21 (84%) lived to at least the next year. As Table 9 and Appendix III show, the lower rate of survival in group 1 is due to the unusually low survival rate of yearling or older birds from 1975 to 1976. All the above survival rates are minimal because they ignore the possibility of undetected survival of marked birds that might have emigrated.

We did not directly observe any predation on fledglings. Postfledging mortality occurs mainly in the 2-3 week period before juveniles can fly strongly, when they seek concealment on the ground or on low perches and are vulnerable to terrestrial predators, including humans and dogs, and to death by exposure.

None of us has ever worked for an extended period in the Neotropics where we saw so few hawks. In the five summer study sessions we saw only one Gray Hawk *(Buteo nitidus)* on the study area; one bird, perhaps the same one each year, was seen only occasionally. Rarely a blackish hawk (species not determined, probably a *Buteogallus*) soared over at high altitude and constituted no threat as a predator, but the Gray Hawk could surely take preflying fledglings. The jays mobbed the Gray Hawk and reacted to its flights over or through the groves with the overhead

predator call (Hardy 1979) and escape flight, suggesting experience with this raptor as a predator. Brown and Amadon (1970) mentioned birds as Gray Hawk prey, specifically listing a parakeet *(Aratinga).* A pair of Mottled Woodowls *(Ciccaba virgata)* were on the study tract and certainly constituted potential predators of juveniles, as we saw jays mob them several times.

We found evidence of predation on three non-nestling jays. O/G-L, an adult female of group 1, was killed in June 1977. We found her flags, a tarsus, and scattered feathers on the ground. O/Bk-R, a fledgling of nest 31. was killed one day after leaving the nest. We found its flags in the nearby jungle, where the bird had moved on the ground. PiBk, a yearling female, was found alive with all remiges clipped. She was obviously a victim of human vandals and probably felled with a slingshot. The first two birds may also have been downed by humans and then eaten by dogs or natural predators. An odd accident was the cause of another death: OO, an adult male in group 1, died by hanging. While foraging it had fluttered upward in pursuit of a prey item and then had fallen slightly, catching its neck in the constricted distal end of a palm bract. Death caused by this occupational hazard must be rare. Evidence is slim and mostly circumstantial, but deaths of yearlings or older birds may be mainly due to humans — specifically boys with slingshots. The boys carry slingshots as they patrol the cornfields to keep out the Great-tailed Grackles that pilfer the corn sprouts.

EMIGRATION AND IMMIGRATION. — The disappearance of birds after fledging gives a maximum mortality figure that undoubtedly includes emigration. Between the nesting seasons of 1975 and 1976, four adults, one yearling, and one young of the year disappeared from group 1, while three adults and two yearlings immigrated to the group. Between 1976 and 1977, four yearling or older birds and four first-year birds disappeared, while one adult immigrated. From 1977 to 1978, two yearlings and six first-year birds disappeared and one yearling and one 2-year-old immigrated to the group. Thus in a 4-year period 22 birds of fledgling age or older disappeared and eight immigrated to group 1. For group 2, the figures are similar: from 1976 to 1977, four yearling or older birds, and five or six first-year birds disappeared, while five yearling or older birds immigrated to the group. In the 1977 to 1978 period, two adults, two yearlings, and seven first-year birds disappeared, while four yearlings joined the group. Thus 20 or 21 disappeared and 9 immigrated in the 3-year period.

Two marked birds are known to have changed groups. PiBK, a female banded as a fledgling in group 3 in June 1975, was found in group 2 in contents of which could not be determined. A few days later the bird was found alive with its wing feathers clipped. Its actual role in group 1 was

never determined accurately, as the nest it was found on had a few days earlier been occupied by an adult female. GPi, a female flagged as an adult in group 3 in 1975, was not detected in 1976, but was found as a breeder in group 2 (nests 35, 44, 58) in 1977 and 1978. No other changes of group membership were known to have occurred among groups 1-5, 1974-78, nor were any marked birds ever found in immediately peripheral groups. Therefore, immigration probably involves saltation beyond neighboring groups.

Most of the birds that immigrated to our study groups were of unknown origin. At the end of field work in late July 1975, all adults and fledglings in group 1 were flagged, and had shown no evidence of nesting behavior for several weeks. Yet in June 1976 four unmarked adult females were present as breeders and two yearlings as helpers. Except for one (XX ad. female, mate of PP, 1976-7) these were flagged as follows: adult females O/G-L, BlBk, Bl/G-L; yearlings PiP, PiW. Subsequently O/G-L was taken by a predator (June 1978), PiW was still a helper as a 2-year-old in 1976 but had disappeared in 1977, and PiP was apparently still a helper as a 3-year-old in 1978. The 1976 field study ended on 28 July with some nests still active in group 2. Therefore we could not tell whether the unmarked yearling found in group 2 in 1977 was hatched in group 2 or had immigrated to it. A pair of unbanded adults, subsequently female Bk/Pi-R and male P/G-R (nests 30, 54), were present as we began study in June 1977. That male is positive evidence of immigration of adult males, as we were certain that at the end of study in 1976 all birds of yearling age or over in group 2 were flagged; apparently females are more likely than males to change groups.

We secured our best evidence for dispersal of young in 1978. In 1977 we banded all 17 fledglings in groups 1 and 2 (Table 10) of which 13 were known to be alive and able to fly in late July. Eight of these were in group 1 and five were in group 2. At that time nesting had ceased in group 1, but group 2 still had six active nests, three of which had late nestlings. We found none of these banded birds in 1978, but group 1 had two unbanded yearlings and group 2 three. The two unbanded yearlings in group 1 substantiate immigation there. The only interpretation that disallows immigration or emigration in group 2 in significant quantities requires the assumption that all five banded young had died and that only unbanded young survived.

Our data do not allow us to state whether adults are more likely than young to disperse to other groups.

BEHAVIOR AND MOVEMENTS OF YOUNG

FLEDGLINGS. — Departure of young from the nest was gradual. During the 1-3 days prior to leaving permanently, the nestlings typically perched

TABLE 10. — History of fledgling San Blas Jays, 1977.

Group 1 nest	Tag code	Wt. (g)	Date fledged	Survived	(Date)
26	PiBk-2	92	4/7 (forced)		
	O/G-L-2	76	4/7 (forced)	yes	(27/7)
	BlO-2	93	4/7 (forced)		
27	G/O-L	84	18/6	yes?	(27/7)
	P/Pi-L	85	18/6	no	
34	Nestlings only	Did not fledge			
36	Bl/O-L	90	27/7	yes	
39	Nest failed, no young				
	(Orphans introduced on 3 July)				
	OO-2	80			
	GG-2	80		yes	
	PiG-2	83			

Group 2	Tag code	Wt. (g)	Date fledged	Survived	(Date)
28	Pi/Pi-R	87	20/6	yes	(27/7)
	Pi/Bk-R	95	20/6	yes	(27/7)
	Bl/Bl-R	86	20/6	yes	27/7
29	O/O-R	101	18/6	yes	27/7
	G/G-R	98	18/6	no	
30	O/P-R	92	18/6	yes	(27/7)
	G/P-R	78	18/6	no	
31	O/Bk-R	84	13/7	no	

(No other nests in group 2 produced fledglings in 1977 before we completed field work for the season.)

on limbs within a few feet of the nest, and returned to the nest several times. When nests are in native trees the young probably climb about in branches up to several meters away, but departure from the immediate nest area in coconut palms usually means rapid descent to the ground. This normally occurred when the young were about 18-20 days old and weighed between 80 and 100 g. All fledglings that survived more than a few days weighed at least 80 g at fledging, and most weighed between 90 and 100 g (Table 10). With no known exceptions in our study, fledglings remained on the ground or within a few meters of it for about the first week after leaving the nest. In this time they moved by running and fluttering. It is important that ground-level vegetation be present for the young to hide in during this period. They would cross bare ground to reach such vegetation, but their detectability, at least to human observers, was greatly decreased if little movement across open ground

was necessary. The adults seemed to urge them toward cover by gathering in hedgerows or trees over such vegetation and calling the young toward protection, rather than landing in the open near them. Fledgling members of a single brood tended to stay together; this is probably why puny nestlings seemingly fledged prematurely, being stimulated to do so by the departure of their stronger siblings and by the rapid decline of feeding visits to lone individuals that stayed in the nest.

By approximately one week after fledging, juveniles could fly a few meters by launching from perches about a meter off the ground, but they tired easily and still could not fly upward. In the second week after fledging, they climbed higher in trees and flew from tree to tree. From this age onward, although they landed clumsily, they remained above ground and flew with increasing strength upward and into the tall palms, but in our general experience they usually stayed from about 3 to 6 m up in dense broadleaved vegetation of hedgerows and jungle areas.

JUVENILE MOVEMENTS: HOME RANGE AND CORE AREA FIDELITY. – Juveniles seldom strayed beyond their communal group home range boundary. This site fidelity was probably a result of the reluctance of their attendants to cross such boundaries. In 1976 we performed two experimental transportations of fledglings that seemed to demonstrate home range exclusivity and fidelity. On 2 July we found three probable sibling fledglings in group 4's home range. After they were flagged, we carried one of them, BkW, in full sight of the attending group of jays into the nearby southeastern portion of group 2's home range. The attendant jays of group 4 followed, scolding, to the boundary (as previously determined) between the two home ranges and no farther. These attendants then silently withdrew. At this time PPi and O/Pi-R of group 2 began mobbing the observers, diving at them and scolding. The fledgling then became silent and stopped struggling. When it was brought back to the group 4 area 10 minutes later, the attendants greeted the approaching human and mobbed him. The fledgling again called and struggled. The following day the same fledgling and two others from group 4 were taken one at a time at 15 min intervals into the same part of group 2's range, about 50 m from group 4. Group 4 members scolded but would not follow into group 2's range. The cries of the young obviously could be heard by their attendants. The young were placed in a shrub at the base of a palm and left alone. Within 15 min of the transportation of the third juvenile, the pair of nest 21 in group 2 was feeding them.

, At about the same time that the young fledged from nest 26 in group 1 in 1977, we introduced three young orphan fledglings (brought to us by local children) to the area. These were adopted immediately by group 1 birds and cared for in a way and with a frequency indistinguishable from that afforded to the group's own offspring. The orphans were still alive at

the close of the summer's study and apparently incorporated into group 1.

These experiments first confirm the reality of home range boundaries and their value against trespass. Second, parents may recognize their own young by their location rather than by means of intrinsic characteristics.

In 1977 experiments involving transport of fledglings in group 2, we discovered that core area boundaries also may prevent adults from following their young. On 18 June the fledglings from nest 30 were carried toward nest 29. The parents followed but refused to enter the core area of nest 29. On 3 July the nestlings of nest 31, with their nest, which had been knocked down in a coconut harvest, were transported to the nest 31-35 core area mutual boundary at the mango tree in the middle of the grove (Fig. 16). The parents would not go beyond that point, and their yearling helper Pi/G-R stopped 10 m beyond the mango. Thus parents and attendants intimately involved in the care of their young, in addition to respecting home range boundaries of the group, also did not follow far from the nest site or near to another pair's nest site, during the preflight juvenile stage.

As the young began to fly well, their wanderings increased. In group 1 all the flying young traveled over most of the home range. In group 2 adults followed flying juveniles without regard to core area boundaries. Young of nests 28, 29, and 30, whose movements were followed carefully for over a month, did not use the entire home range of group 2, at least up to 28 July. This seemingly had nothing to do with core area boundary observance but was simply a result of the large size of the home range itself. Figure 17 shows the movements of Pi/Pi-R, Pi/Bk-R, and Bl/Bl-R, the young of nest 28, and O/O-R and O/P-R, young of nests 29 and 30, respectively, all in 1977. The nest mates of the latter two birds vanished soon after fledging, and the two survivors joined together. They were still together at the end of the study on 27 July. The three birds from nest 28 were banded on 20 June and remained together at least to 27 July. Note that some overlap occurred in the movement of these two groups of young, but they did not share any attendants. The young of nest 28 were attended almost exclusively by their parents and the yearling WBk. Juveniles of nest 29 and 30 were attended primarily by the nest 30 parents. The nest 29 parents relinquished care as if their offspring did not exist, and, like the nest 31 parents that lost their surviving fledgling the day after it left the nest, began a second nest.

Strongly flying juveniles even crossed home range boundaries and were followed by their attendants when portions of the adjacent home ranges into which they wandered had been essentially deserted by the residents. The young of nest 28 were observed in the groups 1 and 5 areas on 23 July, and were being attended by their parents and helpers, but the area of trespass into group 1's range had been virtually vacated by its resi-

MOVEMENT AREAS

▨ JUVENILES· OF N-28

▨ JUVENILES OF N-29,30
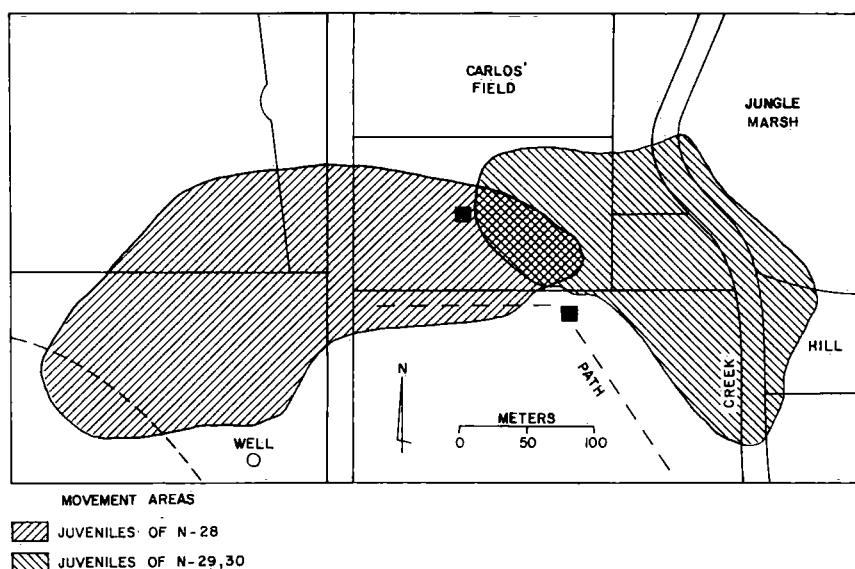
FIGURE 17.   Movements of Pi/Pi-R, Pi/Bk-R, and Bl/Bl-R, the fledglings from nest 28, and O/O-R and O/P-R, fledglings from nests 29 and 30, respectively, in 1977.

dent jays for more than a week, the resident nesters having moved with their fledged young to the western part of their home range. A similar trespass of boundaries occurred between groups 2 and 3 after the outlying nest 30 of group 2 fledged its young in 1977. Because this nest had no protective ground vegetation in its vicinity, the fledglings quickly moved north and east. Within one week thereafter group 3 birds were attending a strongly flying juvenile within 5 meters of nest 30.

As in Yucatan and Bushy-crested Jays, full-grown juveniles of the Southern San Blas Jay that were still being fed regularly by their attendants sometimes visited later nests of the group where nestlings were being fed. Juveniles in groups 1 and 2 were never quite old enough to make such visits before our summer field season ended, but in group 3 in late July 1977, two juveniles visited nestlings at nest 47. At first they merely followed feeders to the nest to beg for food, then they came to the nest in the adults' absence and looked at the nestlings. Within the next few days they progressed to arriving at the nest with food, giving guttural calls characteristic of jays feeding nestlings, and occasionally poking their bills into the nest toward the begging young. It seems likely that had observations continued for several more days, actual feeding by the juveniles would have been seen.

FOOD AND FEEDING HABITS

We did not measure food resources but did make frequent observa-

tions of their existence in time and space and according to habitat during the breeding season. Even though rainless periods of several weeks might have produced a food shortage in a more arid habitat, we saw no evidence of any such shortage in our study areas. Insects such as katydids and small lizards, including *Anolis* sp. and occasionally *Iguana*, seemed to compose the bulk of the foods fed to the young and of the animal portion in the diets of older birds. We frequently saw them catching *Anolis* lizards and insects high on the palm fronds. Insects were taken in herbaceous vegetation as well. We never saw the jays feeding on the fruit of native trees or shrubs; mangos were the dominant vegetable item eaten. Foraging in broadleaved native vegetation, in hedgerows, and the jungle patches was mostly at middle and high levels and, from what we could see, involved animal food. Foraging at low levels occurred in the jungle where the open canopy created thicket undergrowth. We often saw jays visit piles of coconut shells to feed on copra waste. We saw no evidence of vegetable matter being fed to the young, in contrast to the case in Nelson San Blas Jays in Nayarit, Mexico, which brought bits of the fleshy pericarp of oil palm nuts to nestlings (Hardy 1976).

Southern San Blas Jays are omnivorous and highly enterprising in their search for food. It was clear that the palm groves provided not only good nesting places but a considerable proportion of the birds' food. The birds moved along the fronds peering into their crevices and poking with their bills to seize prey. They also diligently searched palm fruit and flower clusters, sometimes hanging upside down or fluttering upward to peer into places difficult to reach. It was more difficult to watch the actual capture of prey when the jays foraged in the hedgerows, dense ground-level vegetation, and jungles. It was our impression that the birds split their time in foraging about equally among palms, herbaceous growth beneath palms, hedgerows, and jungle patches. The birds usually foraged singly or in groups of two or three.

NONBREEDING SEASON

We visited the study area only once in the nonbreeding season, in early December 1976. We found groups 1 and 2 almost completely within their respective summer home ranges. We found no mingling of marked birds from different communal groups except for PiBk, a first-year bird, discussed earlier under Emigration and Immigration. The birds moved in larger and tighter units than was characteristic of them in the breeding season, and at times moved more rapidly. Group 1 birds were once seen just beyond the easternmost part of their summer home range as shown on the maps (Figs. 14, 15) where breeding jays never occurred 1974-1978. Group 2 birds were mainly in that portion of their home range along the creek bed, in the groves beyond, and in the jungle/marsh

area. We counted 20 birds in one loose flock moving through the edge of
the jungle. The birds were mostly high in the trees and were more wary of
us and less vocal than in the breeding season. Consequently, they were
difficult to follow and observe. No evidence suggests an influx of jays from
outside the area or of jays occupying markedly different habitat from that
used in the nesting season.

DISCUSSION

Brown (1974) argued that the various expressions of communal
breeding seen in New World jays are all elaborations upon the retention
of young in their natal territories in "K-selected" species, i.e., those whose
life-history characteristics have shifted toward sedentariness, long life,
and iteroparity, while living at or near the carrying capacity of stable,
mature habitats. He also pointed out that such birds may be expected to
have the capacity for individual recognition, and that retention of certain
aspects of juvenile morphology is common in those species so far known.

All four species of the subgenus *Cissilopha,* the black-and-blue jays,
are communal. They live in flocks year round, with a single breeding pair
per nest (only one female lays in a nest) and helpers, which, depending on
the species, may be of any age from a few months to four or more years.
Our evidence (Hardy 1976; Raitt and Hardy 1976, 1979) suggests that
such groups arise by retention of young within the flock. All species are
probably sedentary and have high annual adult survival rates judging
from the Beechey Jay (Raitt et al., ms) and Southern San Blas Jay (this
paper), and our impressions of the Yucatan Jay (Raitt and Hardy 1976),
Nelson San Blas Jay and Bushy-crested Jay (Hardy 1976). All are also
usually single-brooded (same references). In all four species the yearlings
are morphologically separable from the adults (see Hardy 1973). At least
in the Southern San Blas Jay each adult apparently has unique vocal
characteristics that probably are used in individual recognition (Webber
and Hardy, ms), although there is reason to doubt their ability to
recognize their own young. Table 11 presents a comparative summary of
similarities and differences among the five forms of the *Cissilopha* jays.

The unusually complex nature of communality in the Southern San
Blas Jay, which has large numbers of breeders per group and extensive
mutual helping between breeders, might suggest that communality in this
species is not a variation upon the retention-of-young theme, but has
arisen by aggregation of formerly separate breeding pairs. We believe
that complex ontogeny of plumage and soft-part color, as well as such
postural displays as Upfluffing and Peck-preening (Hardy 1974) that are
associated with the sociality of other communal black-and-blue jays, are
indicators of a long history of communality in this jay as well. Also, if
such groups had arisen as aggregations of neighbors, we would expect to

TABLE 11. — Social breeding characteristics, density, and habitat features in *Cissilopha*.

Form	Social System/Type[1]	Unit Size (Density) in Useable Habitat	Vocal Repertoire[2]	Non-breeders	Age at first breeding	Habitat
Beechey	Simple/S	2-6 (10/km²)	Small	Subad, Ad	3 yrs	Trop. decid. forest
Yucatán	Intermed./P	6-11 (70/km²)	Large	Subad, Ad	3 yrs?	Forest edge with fields
Nelson San Blas	Intermed./P	5-6 (?)	Medium	Subad, Ad	2 yrs	Palm-forest edge
Bushy-crested	Intermed./P	11 (100/km²)	Medium	Subad, Ad	3 yrs?	Coffee plantations under tall forest
Southern San Blas	Complex/P	10-26 (150/km²)	Medium	Subad, Ad	As early as 1 yr, usually 3	Coconut palm plantations, Scrub-woodland edge

[1] See Brown's (1978) social breeding structure classification. S and P stand for one and two or more breeding females per communal unit, respectively.
[2] See Hardy (1979).

see group "membership" based solely on geographic proximity, but in some instances it is not. For example, OW and WO, parents at nests 17 and 18 in group 2 in 1976, fed the nestlings in nest 21 of their group over 200 m away, but did not even approach nest 13 in group 1, only 100 m from their own nests. Presumably group membership is dependent on a history of acquaintance based on an extended family relationship.

Although demographically the black-and-blue jays share the attributes expected in Brown's (1974) early outline, we did not find them living in stable, "mature" habitats (as acknowledged in Brown 1978). Instead, they live in highly modified or disturbed and, in some cases, certainly transient habitat types.

There seems to be a relationship between the "complexity" of communal breeding and the extent of habitat disturbance. Those species in the less-disturbed habitats tend to have lower population densities, smaller groups, fewer breeders per group, and relatively older breeders. Those in the more disturbed habitats have higher population densities, larger groups, more breeders per group, and relatively younger breeders.

The habitats occupied by the jays can be grouped roughly into three classes: (1) "least disturbed"; (2) "moderately disturbed"; and (3) "severely disturbed." The class 1 habitat of the Beechey Jay, while cut-over probably many times, exists in fairly large tracts of continuous habitat, and the jays do not breed in the denser and brushier part of this

habitat, the sort that prevails for perhaps 5 to 10 years after complete raz-
ing, but in the more open, taller portions of the second growth. In short,
they nest in the interior of native woodland that, while immature, is not
mingled or interdigitated to any great extent with cultivated land. The
class 2 habitats, moderately disturbed, are those of the Bushy-crested Jay,
Yucatan Jay, and Nelson San Blas Jay, all of which live in thorough mix-
tures of native vegetation and cultivated crops, both of which the jays use
extensively. The Bushy-crested Jay nests in coffee plantations under a
canopy of tall natural forest trees. The jays may move through more
nearly undisturbed forest along cattle trails, but apparently nest only in
the forest edge or where the understory has been removed and replaced by
the coffee trees (Hardy 1976). Yucatan Jays nest in the edge of native
second-growth woodland interspersed with cornfields, and they forage in
both types of habitat. Nelson San Blas Jays nest where oil palms grow in
plantations or intermixed with native tropical deciduous woodland
(Hardy 1976). Class 3, heavily disturbed habitat of Southern San Blas
Jays, consists mainly of coconut palm groves with only occasional patches
of native growth and fence rows. The jays nest almost entirely in the palm
groves or on the edge of scrubby second-growth broadleaved vegetation
adjacent to the groves.

In Beechey Jays, each communal group has only one breeding pair,
usually but not always accompanied by nonbreeding helpers. Group size
is small, ranging from two to five birds. Population density is low at 10
birds/km² (2 kg/km²). There is never more than one successful nest per
group per year, and only birds three years old or older breed. Vocal reper-
toire is comparatively small (Hardy 1979). The three species in the
moderately disturbed habitats generally breed in larger groups averaging
about 6 in Yucatan Jays, sometimes reaching 11 in Bushy-crested Jays,
and about 5 or 6 in Nelson San Blas Jays, and have more than one pair of
breeders per group. Some, at least, exist at higher densities than do
Beechey Jays. Yucatan Jays (Raitt and Hardy 1976) occurred near Xpujil,
Campeche, at a density of 70/km² (8.5 kg/km²). Data are few on Bushy-
crested Jays, but Hardy (1976) had one group of 11 birds occupying 7.1 ha
(15kg/km²). For Nelson San Blas Jays there are no data on density. Sub-
adult Yucatan and Bushy-crested Jays are not known to breed in the wild,
and subadults may do so in Nelson San Blas Jays only when populations
have been reduced by humans (see Hardy 1976).

In Southern San Blas Jays, occupying the most disturbed habitat,
group size seems to be a minimum of about 10 birds yearling age or more
and can range up to 26. Densities are high (150/km²; 19 kg/km²). Almost
all group members are breeders (up to 10 nests/group have been noted),
2-year-olds sometimes breed, and even 1-year-olds are known to breed,
though rarely. Table 11 summarizes the foregoing comparison.

In discussing the relatively simple sociality and low reproductive effort of the Beechey Jay, Raitt and Hardy (1979) postulated as the underlying cause the very extreme and long dry season of its habitat and consequent low productivity of food resources. What we are postulating here is a parallel factor, which is degree of habitat disturbance and reliance on ecosystems highly influenced by human intervention.

As in the earlier attempt to explain the social characteristics and body size of Beechey Jays as responses to low food supplies, we speculate that an important factor linking greater habitat disturbance with greater population density and greater group size is the increased availability of food prey. We did not measure insect abundance in the jay habitats, though we take some comfort from Janzen's (1973) assertion that all previous attempts to measure such abundances probably were unreliable.

R.P. Balda reviewed this paper in manuscript and commented on the foregoing speculation as follows: "One major point seems to be overlooked here. That is, how 'full' is the available habitat for these birds? If it is not full then young should go off and nest on their own rather than stay and help. Their help should not be necessary if insect and vertebrate productivity is high."

We have no objective, independent way of measuring how full the San Blas Jay habitat is, nor do we know whether helpers help wholly or partly because their efforts increase overall reproduction. Balda's comment does point out the necessity of offering a plausible explanation of how increased population density could result in an increase in group size, instead of merely the addition of more "normal"-sized groups. At least two such explanations are possible, depending upon the factors that govern dispersal in San Blas Jays.

Perhaps helpers will disperse from their home groups unless the habitat is so full of other jays that few or no places exist for them to go, as Balda suggested. Any factor that increased population density would increase the fullness of the habitat. At some point this increased filling of the habitat would result in reduced opportunities for dispersal, and thus at least some growth in group size would occur with the retention of helpers.

Or perhaps the helpers might not disperse even if space was available elsewhere, because of some overriding reason for staying home, such as the protection afforded by living with a larger group of relatives. In this case, population growth, regardless of cause, would automatically result in an increase in group size.

Some within-species comparisons in other communal breeders suggest that habitat productivity or structure can affect group size. For example, Hall's Babblers *(Pomatostomus halli)* prefer to forage in grass and forbs. Brown and Balda (1977) found that group size in these babblers was positively correlated with percent of flock home range having such her-

baceous growth. Gaston (1978) found that larger groups of Common Bab-
blers *(Turdoides caudatus)* were characteristic of local populations of
above average density and implied that greater habitat productivity pro-
motes larger communal group size.

With greater group size, more birds per group (as well as younger
birds) may be allowed to breed because it is more difficult for dominant
birds to suppress breeding by other group members. This proposal re-
quires two conditions: first that the delayed breeding observed in the
black-and-blue jays is not a result of physiological inability to breed but a
socially or habitat-mediated suppression of breeding behavior, and sec-
ond that changes in habitats (such as to cultivated land) that must have
occurred recently could plausibly affect breeding organization of the
birds in such a short time.

Evidence suggests that breeding in communal New World jays can be
suppressed socially. In 1968 Hardy (1976) caged a presumed family group
of six Yucatan Jays consisting of two adults, two 2-year-olds, and two
yearlings. Each year through 1972 the oldest birds, apparently a mated
pair when captured, attempted to breed. Although all the others occa-
sionally handled nest material, none made any coordinated attempt to
build a nest or demonstrated any other evidence of concerted breeding
behavior. In 1972, after the pair again attempted to breed, the other four
birds, by then all adults, were removed to another aviary. Within nine
days, the next oldest male and female paired, built a nest, and produced
their first eggs. Gonads of the nonbreeding 1- to 6-year-old members of
this group were enlarged in the period when the dominant pair was at-
tempting to breed.

Parallels exist in some other communally breeding species. Common
Babblers usually have only one breeding pair per communal group, but
two pairs may breed simultaneously in larger groups, apparently because
of spatial separation that reduces interpair rivalry (Gaston 1978). Fur-
thermore at least the male nonbreeders in communal groups had enlarged
gonads, suggesting their potential for breeding. Similarly Carrick (1972)
found that subordinate females in communal groups of Australian
Magpies *(Gymnorhina tibicen)* are often prevented from breeding by
dominant females, but may nest if they find a site suitably distant from
that of the dominant female. Otherwise, they begin to nest only after the
dominant female is occupied with incubation. Florida Scrub Jays will
breed when 1 year old, given the opportunity. A pair of 1-year-olds bred
in an aviary at the University of Florida, evidently because they had an
exclusive "breeding territory" (Webber, ms). On very rare occasions
yearlings breed in the wild (G.E. Woolfenden, pers. comm.).

The major factors allowing more birds to breed in Southern San Blas
Jay groups may be the abundance of nest sites and food in the palm groves

and the sheer numbers of potential breeders. Greater spatial separation of breeders in larger groups may not be an important factor in this regard. At least the youngest, most subordinate birds seem to create opportunities to breed by temporal rather than spatial segregation from the older birds (Table 5). Furthermore the apparent greater simultaneity of nesting in group 2 probably cannot be attributed to greater spatial segregation in that group, for nest cluster densities were about the same in groups 1 and 2. (The difference of 10 m in the mean inter-nest distance is of doubtful significance.) The apparent difference in simultaneity may itself be an artifact of sampling.

The difference in core area behavior between groups 1 and 2 indicates the degree of flexibility that can exist in the social organization of the Southern San Blas Jay. Group 2, while nesting in clusters of about the same density as those in group 1 (Table 5), was spread out over a larger absolute area, which resulted in a reduced frequency of contact between many members of the group, reflected in the lower C.I. and C.U. in group 2 than in group 1. Also, group 2's home range was compartmentalized into several clumps separated by relatively large patches of jungle, stream-side vegetation, and grove areas unsuitable for nesting (Fig. 1). Group 1's home range, in contrast, was in much more uniform palm groves. In group 2 the jungle patches greatly reduced visibility within the home range, which may be one reason why breeders remained relatively close to their own nests. The reduction of contacts between breeders in the group thus resulted in a form of quasi-territorial behavior within the group and an increased frequency of ritualized agonistic displays. Even greater plasticity in social organization has been demonstrated by Stacey and Bock (1978) in the Acorn Woodpecker *(Melanerpes formicivorus)*, in which nonmigratory communal groups live side by side with migratory unaided pairs in southeastern Arizona.

LITERATURE CITED

Brown, J.L. 1974. Alternate routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. Am. Zool. 14: 63-80.
_____. 1978. Avian communal breeding systems. Ann. Rev. Ecol. Syst. 9: 123-155.
_____, and R. P. Balda. 1977. The relationship of habitat quality to group size in Hall's Babbler *(Pomatostomus halli)*. Condor 79: 312-320.
Brown, L., and D. Amadon. 1968. Eagles, hawks and falcons of the world. Vol. 2. New York, McGraw-Hill Book Co., 945 p.
Carrick, R. 1972. Population ecology of the Australian Black-backed Magpie, Royal Penguin, and Silver Gull; pp. 41-99 in Population ecology of migratory birds: A symposium. U.S. Dept. Inter. Wildl. Res. Rept. 2: 278 p.
Gaston, A.J. 1978. Ecology of the Common Babbler *Turdoides caudatus*. Ibis 120: 415-432.

Hardy, J.W. 1969. A taxonomic revision of the New World jays. Condor 71: 360-375.
_____. 1973. Age and sex differences in the black-and-blue jays of Middle America. Bird-Banding 44: 81-90.
_____. 1974. Behavior and its evolution in neotropical jays (Cissilopha). Bird-Banding 45: 253-268.
_____. 1976. Comparative breeding behavior and ecology of the Bushy-crested and Nelson San Blas Jays. Wilson Bull. 88: 96-120.
_____. 1979. Vocal repertoire and its possible evolution in the black-and-blue jays (Cissilopha). Wilson Bull. 91: 187-201.
_____, and R. J. Raitt. 1976. Ecology and evolution and communal habits in the black-and-blue jays (Cyanocorax, Cissilopha). Int. Ornithol. Congr. 16, Canberra, Abstr.: 105.
_____. 1977. Relationships between the two races of the San Blas Jay Cyanocorax sanblasiana. Bull. British Ornithol. Club 97: 27-31.
Janzen, D.H. 1973. Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54: 687-701.
Lamb, C.C. 1944. Grackle kills warbler. Condor 45: 245.
Olivares, OFM. A., and J.A. Munves. 1973. Predatory behavior of Smooth-billed Ani. Auk. 90:891.
Raitt, R.J., and J.W. Hardy. 1976. Behavioral ecology of the Yucatan Jay. Wilson Bull. 88: 529-554.
_____. 1979. Social behavior, habitat, and food of the Beechey Jay. Wilson Bull. 91: 1-15.
Skutch, A., in A.C. Bent. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211:335-350.
Stacey, P.B., and C.E. Bock. 1978. Social plasticity in the Acorn Woodpecker. Science 202:1298-1300.
Wetmore. A. 1927. The birds of Porto Rico and the Virgin Islands (Psittaciformes to Passeriformes). New York Acad. Sci. 9:409-598.
Woolfenden. G.E., and J.W. Fitzpatrick. 1978. The inheritance of territory in group-breeding birds. Bioscience 28:104-108.

APPENDIX I

COMPOSITION AND HISTORY OF SAN BLAS JAY GROUPS 1 AND 2[1]

	Color Code[1]	Year Marked	Age When Marked	Sex (Crit.)	ROLES				
					1974	1975	1976	1977	1978
GROUP 1									
1	00	74	Ad	♂ (Role)	A-1	P?-Nx[2] H-Nx, 3, 5, 9	H-13, 15	Found Dead June[3]	
2	PiPi	74	Ad	♀ (BP)	P?-1				
3	BkBk	74	Ad	♂ (Role)	P?-1	P-9, H-5?			
4	WW	74	Ad	♀ ? (Role 75)	A-1	P?-Nx	A-BlP H-Nx, 13, 15		
5	BlBl	74	Ad	?	A-fl				
6	XX	-	Ad	♀ (Role)	P-2				
7	XX	-	Ad	?	A-3				
8	XX	-	2	?	A-3				
9	GG	74	1	♂ (Role)	?	H-5	H-12, 13, 14?	P-27 H-26	A-fl?
10	PP	74	1	♂ (Role)	A-fl	H-5,9	P-15 H-13	P-34 H-26, 27, 36	P-Nx
11	PiG	74	1	♂ (Role)	?	P-3 H-4, 5, 9	P-Nx? P of O/Pi-L? H-13, 15	P-36 H-26, 27	P-50
12	XX	-	1	?	A-3				
13	XW	74 sib	0	?	fl Nx				
14	XPi	74 sib	0	?	fl Nx	H-3, 5, 9			
15	XG	74 sib	0	?	fl Nx				
16	XO	74 sib	0	?	fl Nx				

17	OPi	75	Ad	♂ (Role)	P-5 H-9	P-12 H-13	P₂-26⁴ H-36	P-48
18	BlO	75	Ad	♂ (Role)	P-4 H-3, 5, 9	P-13 H-Nx fl		
19	GBl	75	Ad	♀ (Role)	P-4 H-5, 9?			
20	PiO	75	Ad	♀ (Role)	P-5 H-3, 9			
21	XX	-	Ad	♀ (Role)	P-9			
22	GW	75	1	?	H-5, 9			
23	XX	-	1	♀ (Role)	P-3			
24	GO	75	0	?	5 fl			
25	OBL	75	0	♂ (Role)	5 fl	H-12, 13, 15	P₁-26⁴ P-39	P-Nx? with BlBk?
26	Bl/G-L	76	Ad	♀ (Role)		P-12	P₂-26⁴	P-48 fl
27	XX	76	Ad	♀ (Role)		P-15	P-34 H-36	
28	O/G-L	76	Ad	♀ (Role)		P-13 H-12	Predatorized June	
29	BlBk	76	Ad	♀ (Role)		P?-Nx	P₁-26 P-39	P-Nx? with OBl?
30	PiP	76	1	?		H-12, 13, 15 H-BlP fl		
31	PiW	76	1	?		H-Nx, 12, 13	H-26, 27, 34?, 36	A-fl
32	PiBK	75	0	♀ (Role)	Group 3 fl	P-14? sitter, dead Nx fl		
33	BlP	76	0	?		13 fl		
34	PiPi-2	76 sib ⎤	0	?		13 fl	H-27	
35	BlBl-2	76 sib ⎬	0	?		13 fl	H-27, 34, 36	
36	Pi/Bl-L	76 sib ⎦	0	♂?		13 fl	H-26,27	A-fl

APPENDIX I (continued)

COMPOSITION AND HISTORY OF SAN BLAS JAY GROUPS 1 AND 2[1]

	Color Code[1]	Year Marked	Age When Marked	Sex (Crit.)	ROLES			
					1975	1976	1977	1978
37	O/Pi-L	76	0	?		Nx fl		
38	Bl/Pi-L	76 sib	0	?		12 fl		
39	G/Bl-L	76 sib	0	?		12 fl		
40	XX	-	Ad	♀ (Role)			P-36	
41	P/O-R	77	Ad	♀ (Role)			P-27 H-26	P-50
42	PiBk-2	77 sib	0	?			26 fl	
43	O/G-L-2	77 sib	0	?			26 fl	
44	BlO-2	77 sib	0	?			26 fl	
45	G/O-L	77 sib	0	?			27 fl	
46	P/Pi-L	77 sib	0	?			27 fl	
47	Bl/O-L	77	0				36 fl	
48	XX	-	2	?				A-fl
49	XX	-	1	?				A-fl
GROUP 2					1975	1976	1977	1978
1	OG	75	Ad	?	?	H-15?, 21		
2	WO	75	Ad	♂ (Role)	H-8?	P-18, H-21	P-28 H-29	P-51 fl
3	OW	75	Ad	♂ (Role)	?	P-17, H-18, 21	P-29, 45, H-28, H-30 fl	P-52 fl
4	PPi	75	Ad	♀ (Role)	?	P-21	P-31, 46	P-57
5	OP	75	2	♂ (Role)	?	P-22, H-23	P-33 H-29,30	P-56

6	PO	75	Ad	♀ (BP)	H-8?	H-28 fl	H-30? seen once	
7	OBk	75	Ad	♂ (Role)	?	H-24?	P-37, H-29 30 fl	P-55
8	GPi	75	Ad	♀ (Role)	Group 3	?	P-35, 44	P-58
9	BkO	75	Ad	?	H-8	H-18		
10	GP	75	Ad	♀ (Role)	?	P-23 H-24	P-40, 43	P-59
11	BlW	75	1	?	H-8	H-18	P-32, 41 H-28? 30, 31, 38	H-59
12	PiX	75	1	?				
13	PG	75	0	?	9 fl			
14	BlG	75	0	?	6 fl			
15	PiBK	76	Ad	♀ (BP)		H-22, 23		
16	WBl	76	Ad	♀ (Role)		P-18	P-28, H-29	P-51 fl
17	Pi/Bl-R	76	Ad	♀ (Role)		P-22, H-23 fl H-24	? seen with P's of 32 twice	
18	G/O-R	76	Ad	♂ (Role)		P-24, H-23	P-38, H-30 31 fl	P-59, H-58
19	O/Pi-R	76	Ad	♂ (Role)		P-21	P-31	P-57
20	Pi/O-R	76	Ad	♀ (Role)		P-23, H-22	P-37, 46, H-29, 30 fl	P-55
21	O/Bl-R	76	Ad	♂ (Role)		H-22, 23	P-40, 43 H-29	
22	XX	-	Ad	♀ (Role)		P-17 H-18, 21? 23?	P-29, P-45, H-28	P-52 fl
23	XX	-	Ad	♀ (Role)		P-24, 21? 23? H-18		
24	BlPi	76	1	♀ (Role)		H-18, 23?	P-33, H-28, 29	P-56
25	Bl/O-R	76	1	?		H-22, 23		

APPENDIX I (continued)

COMPOSITION AND HISTORY OF SAN BLAS JAY GROUPS 1 AND 2[1]

	Color Code[1]	Year Marked	Age When Marked	Sex (Crit.)	ROLES			
					1975	1976	1977	1978
26	Bl/G-R	76	1	♂ (Role)		H-22, 23	H-30, 33, 29 fl	P-53
27	WBk	76 sib⌐	0	?		18 fl	H-28, 29	H-51, 52
28	WPi	76 sib⌐	0	?		18 fl		
29	Pi/G-R	76 sib⌐	0	?		22 fl	H-29, 30, 31, 33, 38	H-57
30	G/Pi-R	76 sib⌐	0	?		22 fl	H-31 seen once	
31	O/G-R	76	0	?		21 fl		
32	PiBk	76 sib⌐	0	?		23 fl		
33	Bl/Pi-R	76 sib	0			23 fl		
34	G/Bl-R	76 sib⌐	0	?		23 fl		
35	XX		Ad	♂ (Role)			P-35, 44	P-58
36	P/G-R	77	Ad	♂ (Role)			P-30, H-29, 37, 38?	P-54
37	Bk/Pi-R	77	Ad	♀ (Role)			P-30, H-29 fl	P-54
38	XX	-	2	♂ (Role)			P-32, 41 H-31? 38, 40	
39	Bk/O-R	77	1	♀ (Role)			P-38	
40	Pi/Pi-R	77 sib⌐	0	?			28 fl	
41	Pi/Bk-R	77 sib	0	?			28 fl	
42	Bl/Bl-R	77 sib⌐	0	?			28 fl	
43	O/O-R	77 sib⌐	0	?			29 fl	
44	G/G-R	77 sib⌐	0	?			29 fl	
45	O/P-R	77 sib⌐	0	?			30 fl	
46	G/P-R	77 sib⌐	0	?			30 fl	

47	O/Bk-R	77	0	?	31 fl (Predatorized)
48	XX	-	Ad	♀ (Role)	P-53
49	XX	-	1	?	with OW, XX, WO, WBl
50	XX	-	1	?	with OW, XX, WO, WBl
51	XX	-	1	?	with G/O-R, GP, and BlW
52	XX	-	1	?	with O/Pi-R, and PPi

[1]Code: color flag tarsal markers. A slant mark between two colors indicates they were on the same leg, designated by a suffix "L" or "R." A suffix numeral indicates that a bird dead or long missing was previously marked with this combination. X means no band. Sex (crit.): birds were sexed by role, or brood patch (BP). Roles: P = parent; H = helper; A = attendant, whether helper or parent not known; fl = fledgling; numerals = number(s) of the nest(s) at which role was played.
[2]Nx = undiscovered nest; ? = designation probable but not based on "best" information.
[3]Probably dead several days: as a result, could not be sexed by gonadal condition.
[4]The genetic parent P₁ roles and surrogate parent roles P₁ of birds at nest 26, 1977, are discussed in the text on p. 26.

APPENDIX II

SUMMARY OF SAN BLAS JAY NESTS AND ATTENDANTS OF GROUP 1, 1975-7 AND GROUP 2, 1976-7

Group 1, 1975	Nest by Number in Temporal Order, Left to Right			
	5[1]	9	4	3
Breeding Pair	♂ ♀ OPi, PiO	♂ ♀ BkBk, XXad	♂ ♀ BlO, GBl	♂ ♀ PiG, XXyrl
Attendants	OPi, PiO, PiG, OO, GBl, BlO, GW, PP, GG, XPi, BkBk?	BkBk, XXad, GBl, BlO, PiO, PiG, OPi, OO, XPi, GW, PP	BlO, GBl, PiG	PiG, XXyrl, GBl PiO, BlO, OO, XPi

Group 1, 1976	Nests by Number in Temporal Order Left to Right					
	Nx[2]	14	16	13	12	15
Breeding Pair	♂ ♀ PiG, BlBk	♂ ♀ ??	♂ ♀ OO, ?	♂ ♀ BlO, O/G-L	♂ ♀ OPi, Bl/G-L	♂ ♀ PP, XX ad
Attendants	PiG, BlBk, OO, WW, BlO, PiW, others?	PiBk[3]	OO, ?	BlO, O/G-L, OO WW, OPi, OBl, PiG, GG, PiP, PiW, PP	OPi, Bl/G-L, PiP, OBl, PiW, O/G-L, GG	PP, XXad, WW, OBl, PiP, PiG, OO

Group 1, 1977	Nests by Number in Temporal Order, Left to Right				
	27	26	34	36	39
Breeding Pair	♂ ♀ GG, P/O-R	♂ ♀ OBl, BlBk[4]	♂ ♀ PP, XXad	♂ ♀ PiG, XXad	♂ ♀ OBl, BlBk[1]
Attendants	GG, P/O-R, PiG, PP, PiW, PiPi-2, BlBl-2, Pi/Bl-L	OBl, BlBk, OPi, Bl/G-L[4], PiG, GG, BlBl-2, PiW, Pi/Bl-L, P/O-R, PP	PP, XXad, BlBl-2, PiW	PiG, XXad, OPi, BlBl-2, PP, PiW, XXad of N-34	OBl, BlBk

Group 2, 1976	Nests by Number in Temporal Order, Left to Right					
	17	18	21	23	22	24
Breeding Pair	♂ ♀ OW, XXad	♂ ♀ WO, WBl	♂ ♀ O/Pi-R, PPi	♂ ♀ GP, Pi/O-R	♂ ♀ OP, Pi/Bl-R	♂ ♀ G/O-R, XXad
Attendants	OW, XXad	BlW, XXad, WO, WBl, OW, XXad, BkO, BlPi	PPi, O/Pi-R, XXad, XXad, OG, WO, OW	GP, Pi/O-R, O/Bl-R, Bl/G-R, OP, Pi/Bk-R, G/O-R, BkPi, XXad, Bl/O-R, XXad, BlPi? (or Pi/Bl-R)	OP, Pi/Bl-R, Bl/O-R, BkPi, Bl/G-R, Pi/O-R, O/Bl-R	GP, OBK?, Pi/Bl-R, G/O-R, XXad

APPENDIX II (continued)

SUMMARY OF SAN BLAS JAY NESTS AND ATTENDANTS OF GROUP 1, 1975-7 AND GROUP 2, 1976-7

Group 2, 1977	Nest by Number in Temporal Order, Left to Right				
	28	29	30	31	32
Breeding Pair	♂ ♀ WO, WBl	♂ ♀ OW, XXad	♂ ♀ BkPi, P/G-R	♂ ♀ O/Pi-R, PPi	♂ ♀ XX 2 yr, BLW
Attendants	WO, WBl, WBk, XXad, BlW? OW, BlPi	OW, XXad, WO, OBk, WBl, O/Bl-R, P/G-R, Pi/O-R, OP, Bk/Pi-R P/G-R, BlPi, Bl/G-R, WBk,	Bk/Pi-R, P/G-R, PO?, G/O-R, OP. BlW, Bl/G-R, OW, Pi/G-R, OBk	O/Pi-R, PPi, G/Pi-R,Pi/G-R, BlW, G/O-R, XX 2 yr?	XX 2 yr, BlW, Pi/Bl-R?

Group 2, 1977	Nests by Number in Temporal Order, Left to Right				
	33	35	37	38	40
Breeding Pair	♂ ♀ OP, BlPi	♂ ♀ XXad, GPi	♂ ♀ OBk, Pi/O-R	♂ ♀ G/O-R, Bk/O-R	♂ ♀ O/Bl-R, GP
Attendants	OP, BlPi, Bl/G-R, Pi/G-R	XXad, GPi	OBk, Pi/O-R, P/G-R	G/O-R, Bk/O-R, BlW, XX 2 yr, Pi/G-R, P/G-R?	O/Bl-R, GP, XX 2 yr (mate of BlW)

	Nests by Number in Temporal Order, Left to Right				
Group 2, 1977	41	43	44	45	46
Breeding Pair	♂ ♀ XX 2 yr, BlW (See N-32)	♂ ♀ O/Bl-R, GP (see N-40)	♂ ♀ XXad, GPi (see N-35)	♂ ♀ OW, XXad (see N-29)	♂ ♀ O/Pi-R, PPi (see N-31)
Attendants	XX 2 yr, BlW	O/Bl-R, GP	XXad, GPi	OW, XXad	O/Pi-R, PPi

[1] A sixth, earlier, nest was undiscovered, having fledged at least 1 young (found dead) prior to our arrival at study site. Nucleus pair may have been OO and WW.
[2] Nest X not found prior to fledging. Though differing greatly in size, 2 fledglings found shared same putative parents.
[3] PiBk began to sit on nest 14 after its apparent desertion by unmarked adult female, PiBk was vandalized, see text p. 36.
[4] OBl and BlBk were the pair when the nest was discovered. But later, OPi and Bl/G-L had replaced them, the latter being found incubating. See text, p. 26, for discussion.

APPENDIX III
Individual Annual Survival, San Blas Jay Group I

APPENDIX III   Continued

Individual Annual Survival, San Blas Jay Group 2

1975   1976   1977   1978

Banded 1975

Adults
- O G
- W O
- O W
- P Pi
- P O
- O Bk
- Bk O
- G P

2 yr. old – O P

Yearlings
- Pi X
- Bl W

Fledglings
- P G
- Bl G

Banded 1976

Adults
- Bk Pi
- W Bl
- Pi/Bl-R
- G/O-R
- O/Pi-R
- Pi/O-R
- O/Bl-R

Yearlings
- Bl Pi
- Bl/O-R
- Bl/G-R

Fledglings
- W B K
- W Pi
- Pi Bk
- Bl/Pi-R
- G/Bl-R
- O/G-R
- G/Pi-R   ?
- Pi/G-R

Banded 1977

Adults
- G Pi
- Bk/Pi-R
- P/G-R

Yearling – Bk/O-R

Fledglings
- Pi/Pi-R
- Pi/Bk-R
- Bl/Bl-R
- O/O-R
- G/G-R
- O/P-R
- G/P-R
- O/Bk-R

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCI-ENCES SERIES, may be in any field of biology. Manuscripts dealing with natural history of systematic problems involving the southeastern United States or the New World tropics are solicited especially. Manuscripts should be of medium length—circa 35 to 200 pages (10,500-16,000 words). Examination for suitability is made by an Editorial Board.

The BULLETIN is distributed worldwide through institutional subscriptions and exchanges. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this the author(s) receive(s) 50 copies free, and he may purchase additional separates at cost if ordered when page proof is returned. The author is also responsible for any charges incurred for alterations made by him on galley or page proofs. The Museum will send an invoice to the author for this amount upon completion of publication.

PREPARATION OF MANUSCRIPT

Contributors should consult recent numbers of the BULLETIN for preferred style and format. Highly recommended as a guide is the CBE Style Manual, 3rd Edition, 1972 (Washington, D.C., Amer. Inst. Biol. Sci.).

MSS must be submitted in duplicate (please no onionskin) and satisfy the following minimal requirements: They should be typewritten, double-spaced (*especially* tables, figure captions, and "Literature Cited"), on one side of numbered sheets of standard (8-1/2 × 11 in.) bond paper, with at least one-inch margins all around. Figure legends and tables should be typed on separate sheets. All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All illustrations should have a cover sheet. All lettering will be medium weight, sans-serif type (e.g. Futura Medium, News Gothic) in cutout, dry transfer, or lettering guide letters. Make allowance so that after reduction no lowercase letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm high. The maximum size for illustrations is 8-5/8 × 14 in. (twice typepage size); illustrations should not be less than typepage width (4-5/16 in.). Designate the top of each illustration and identify on the back with soft pencil by author's name, MS title, and figure number.

All manuscripts not submitted in BULLETIN format will be returned to the author for retyping.

Manuscripts and all editorial matters should be addressed to:
  Managing Editor of the BULLETIN
  Florida State Museum
  Museum Road
  University of Florida
  Gainesville, FL 32611