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BEHAVIORAL ECOLOGY OF THE YUCATAN JAY

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Prominent among bird groups possessing highly developed cooperative social systems are the New World jays (Brown 1974). Recent studies by Brown (1972) of *Aphelocoma ultramarina* and Woolfenden (1973, 1975) of *Aphelocoma coerulescens coerulescens* have revealed a high degree of sociality in those forms. Cooperative breeding also occurs among the black-and-blue jays of the subgenus *Cissilopha* (genus *Cyanocorax*, fide Hardy 1969), as recently shown by Hardy (1976) for the northern form of the San Blas Jay, *Cyanocorax sanblasiana nelsoni*, of western Mexico and Bushy-crested Jay, *C. melanocyanea*, of Central American highlands. As our results presented here will demonstrate, the Yucatan Jay, *C. yucatanica*, is also highly social and a cooperative breeder.

METHODS

Preliminary field work in the vicinity of Xpujil and Zoh Laguna, Campeche, Mexico (18°35′N, 89°26′W), by Hardy in April 1968 gave indications of the social nature of Yucatan Jays. Intensive studies were undertaken of the species in the same area in the breeding seasons of 1972 and 1973 and in the intervening winter. A field party of 5 persons studied nesting from 7 June to 2 July 1972, and a group of 4 studied winter behavior from 7 to 13 January 1973. Nesting was again studied in 1973, by 1 field worker on a part-time basis beginning 22 May and by 5 additional workers beginning on 3 July; the entire party departed from the study area by 30 July. Jorge E. Orejuela, a member of the field party, also collected specimens for stomach analysis in 1974.

The field work was concentrated in a strip of apparently highly favorable jay habitat along the 9.5 km of narrow unpaved road from Xpujil (on Mexico Highway 186) north to Zoh Laguna, a small lumbermill town. During the breeding season the primary effort was to locate as many nests as possible along the road and to observe behavior at the nests. Special attention was given to determining the number of individuals attending the nests, their sex and age, and their relative contribution to the several phases of nest attendance. We noted behavioral interaction among birds whenever they were observed and attempted to determine something of the movements and foraging behavior of the flocks (once it became apparent that the breeding social unit in this species is, indeed, a flock).

Yucatan Jay *(Cyanocorax yucatanica)*. Upper left, adult (4 years or older); upper right, juvenile; lower left, 2-year-old; lower right, yearling. The 2-year-old bird is in the Up-fluffing display. Painting by Nancy Halliday, Florida State Museum.

In pursuing these approaches, frequent and extended periods were spent observing nests and recording activity; locations of nests and of flocks were noted and mapped, and as many birds as possible were captured, marked, and released. Capture of the birds proved to be difficult. We failed in attempts to use wire ground traps; all birds marked were captured in mist nets: a few near nests in the breeding season, and 9 adjacent to foraging sites at edges of milpas in January. Each captured bird was marked with a distinctive combination of colored plastic (Saflag) flags about 1.5 cm wide and 5.0 cm long, 1 attached by a metal eyelet to each leg. Sex of birds captured in January was determined by laparotomy; in the breeding season this procedure was avoided because of the risk.

Data on age differences in behavior and age composition of groups were based on differences in phenotype of several age classes, as described by Hardy (1973). The color plate preceding this paper depicts the 4 prominent age classes, juvenile, first year, second year, and adult (3-year-olds, here called adults, differ from older birds in having whitish inner bill surfaces).

In January 1973 we concentrated on capturing jays and observing the sizes, age composition, and locations of flocks. Additional details of methods are discussed below.

RANGE AND HABITAT

General description from literature.—The Yucatan Jay occurs throughout the Yucatan Peninsula (Paynter 1955), in the adjacent Mexican state of Tabasco (Miller et al. 1957: 119–120), in the northern half of Belize (Russell 1964:134), and in the Peten district of Guatemala (Land 1970:243). Our study area is approximately in the geographical center of this range.

Literature reports of habitat occurrence and abundance give scant information but do indicate only slight variation except in Belize. For the Peninsula generally, Paynter (1955) says that the race *C. y. yucatanica* is "most common in the region of deciduous forest" but that it occurs occasionally in coastal scrub; for the southwestern race, *C. y. rivularis*, he gives rain forest as the habitat. Judging from his vegetation map and accompanying descriptions it seems that the species occurs in virtually all forested areas of the Peninsula. Edwards (1972:167) reports it as "very common" and occurring "in dense scrubby woodland." In the Peten it is reported by both Land (1970) and Smithe (1966:232) as occurring in "tintal" forest (see beyond for a description of this forest type). Of its occurrence in Belize, Russell (1964) reports that it is uncommon and that "Densely overgrown 'broken pine ridge' and the swampy regions that sometimes border these pinelands are its usual habitat. One specimen was taken several miles from pinelands in dense second growth."

Study area.—The climate of our study area is relatively warm, with rather slight variation in temperature. Freezing temperatures occur rarely if ever. Annual rainfall averages 1025 mm, of which about 80% falls in the months May–October. Monthly mean temperatures (°C) and rainfall (mm), January through December, based on the years 1965–1972 were: 20.8, 57; 21.5, 32; 24.0, 22; 25.7, 22; 27.2, 140; 26.3, 154; 25.4, 97; 25.3, 125; 25.9, 185; 24.7, 100; 22.1, 46; 21.8, 32. These data for Zoh Laguna, are from the Oficina de Climatológia, Secretaría de Recursos Hidráulicos, República de México. Precipitation falls in 2 distinct modes: typical afternoon tropical thunderstorms and prolonged drizzle and downpour acompanying fronts or cyclonic storms, with shifting winds and fog. The latter sometimes last 2 days and bring substantial moisture to the area. During our field work in June 1972 the relative humidity was between 90 and 100% for most of each day but dropped to around 80% in mid-day. The elevation of the area is approximately 250

m. The topography is relatively flat, with occasional low ridges. Apparently because of the nature of the underlying limestone substrate, there is very little surface drainage, and there are no streams or canyons of any significance in the immediate vicinity. In the rainy season standing water accumulates in numerous scattered small depressions.

The vegetation of the region is a mosaic of dense forest, cultivated fields (milpas), and old fields in various stages of secondary succession. The vegetation of the Yucatan Peninsula, including the forests of eastern Campeche, has been variously classified and generally described in several earlier works (Paynter 1955, and others cited therein). More recently Pennington and Sarukhan (1968) gave useful descriptions of the forest types. From them it appears as if the forests of our study area are of 1 or a mixture of 2 types: "selva mediana subperennifolia" and "selva baja subperennifolia." *Brosimium alicastrum*, *Manilkara zapota*, *Chrysophila argentea*, and *Swietania macrophylla* are all listed as principal species of the former type and all occur in our area. Of the similarly abundant tree species of the selva baja, *Bucida buceras*, *Coccoloba cozumelensis*, *Croton reflexifolius*, and *Metopium brownei* were all identified on our study area. On the basis of the generally low stature (approximately 10 m) of the trees and of the numerous areas of poorly drained, inundated substrate, the Xpujil-Zoh Laguna forests are more nearly the selva baja type. We did not identify the main species of that forest type, the tintal, *Haematoxylum campechianum*, but our study of the vegetation did not stress species occurrence and it could have been common and still have escaped our identification. It is also possible that the species has been decimated by selective cutting.

We measured vegetation structure using methods modified from James and Shugart (1970). Data collected include density and basal area (at breast height) of trees, canopy cover, and density of woody stems of shrubs and vines (also at breast height) on 5 circular plots of 100 m^2. In order to sample the forest most heavily used by the jays we located the plots as close to nest trees as possible while including only intact forest. All trees (woody stems 2.0 cm dbh or greater) were measured, but species were not differentiated. Cover was estimated by sighting through a vertical tube with crosshairs, held at eye height, on 20 points at 1-m intervals on 2 randomly selected diameters of each plot. Woody stems of vines and shrubs (less than 2.0 cm dbh) were counted in each of two 2-m wide transects along randomly selected diameters of each plot.

The mean number of trees per m^2 was 1.0 (range 0.8–1.2). The basal area (cm^2) of trees per m^2 was 26.5 (range 19.8–40.9). The percent cover was 73 (range 45–90) and the number of shrubs and vines per m^2 was 1.9 (range 1.5–2.5). Most of the trees were small; over 50% of them in each plot were less than 4.0 cm dbh. Our impressions of high density were confirmed by the heavy canopy cover and by the occurrence of an average of nearly 3 woody stems per m^2. This structure of the forest is a reflection of its secondary character. For centuries it has been subject to milpa agriculture. This type of agriculture continues to the present, with an additional disturbance due to selective logging. Turner (1974) describes the similar nature of classical Mayan agriculture in the area centering about Xpujil.

The forests of the area were fully leafed out during all of our stay in July 1973 and by the end of June 1972. In April 1968 most of the trees were almost completely bare (Fig. 1D), and many were bare or partly so at the time of our arrival in early June 1972, leafing out only after the onset of frequent rains (Fig. 1C). In January 1973, during a relatively wet winter, full foliage was general. From these observations and from the use of the word "subperennifolia" to classify forests of the region by Pennington and Sarukhan (1968), it seems likely that most of the trees are facultatively deciduous, normally dropping their leaves in the autumn and growing them again after the onset of

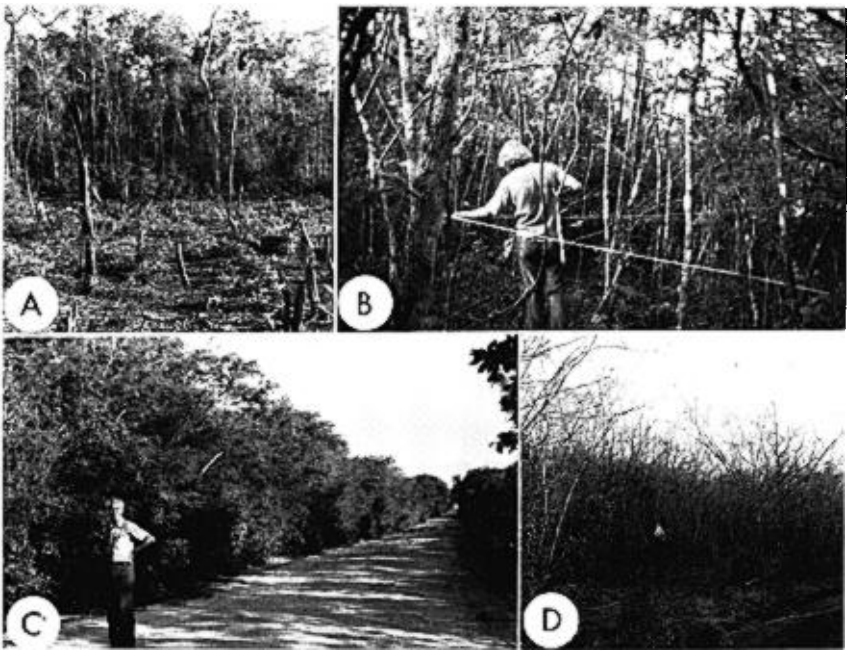

FIG. 1. Photographs of the main study area showing: A, newly cleared milpa in 1973, where forest like that in background existed in 1972; B, interior of the forest, with quadrat being laid out; C, Xpujil-Zoh Laguna road, with Yucatan Jay nesting habitat on both sides; D, dry season aspect of the jay habitat.

rains in the early summer, but retaining them for longer periods when soil moisture remains high.

ANNUAL CYCLE

The social organization and other activity of the Yucatan Jay vary seasonally, with an orderly progression of changes. Our central interests in this study were the events of the breeding season: nest-building, incubation, and care of nestlings and fledglings. Social organization and ecology in the nonbreeding period were also of some interest and importance in facilitating our understanding of the significance of characteristics of the breeding biology of Yucatan Jays. Our approach in this major section is to consider in turn the various phases of the annual cycle, beginning arbitrarily with behavior in the pre-reproductive season, then considering several consecutive aspects of breeding, and ending with a brief description of jay social structure in winter.

Pre-reproductive Period

Our studies do not include work at the time of the transformation of large winter aggregations of jays (see p. 547) into the smaller ones typical of pre-reproductive and reproductive periods. This breakup occurred prior to early April in 1968, a year characterized by a fairly dry winter season, no rain in March or April, and a virtually complete leaf fall in the study area. The period 3–13 April was clear and windy, with temperatures daily reaching the low 30's C. Yucatan Jays were studied almost daily, mainly in the woodland within 1 km of the north edge of Zoh Laguna. Two flocks of fewer than 10 birds (usually counted as "6 or 7" in field notes) inhabited this woodland. They usually occupied discrete areas. A count of about 20 unmarked birds, presumably the total of these flocks, was seen on one occasion attending a swarm of army ants (species unknown) from just after dawn to late morning (see Hardy 1974a). Each of the 2 smaller flocks contained first-year individuals. A flock of about 10 birds was watched twice 9.5 km NW of Zoh Laguna. It also contained at least 2 first-year birds.

Until 16–18 April no observations made of these birds suggested the onset of reproductive behavior; that is, except for group size, behavior was seemingly random wandering within a consistent area, foraging, and resting, at which times allopreening and social "Up-fluffing" displays were evident (Hardy 1974b).

Testes of 3 males taken in this period were enlarged to the size we found in the breeding season in 1972. Those of 2 adults taken by Hardy on 4 and 8 April, respectively (MLZ 65835, JWH 614, not preserved), measured 16 × 10 and 14 × 10 mm and a third adult taken by Kenneth C. Parkes on 6 April (Carnegie Museum 143272) measured 14 × 7 mm. Yet ovaries of 4 females taken in this same period were small. An adult and a yearling female collected 11 km E Ciudad Campeche on 31 March had a slightly enlarged ovary with ova to 2 mm and a small ovary with ova to 1 mm, respectively. An adult female (CM 143292) taken by Parkes on 8 April also had ova to 2 mm. In Hardy's captive flock a 4-year-old female had ova 0.25–0.50 mm on 9 April 1971 and laid an egg in the first week of May, and a 4-year-old male had 10 × 5 mm testes on 5 April 1971. Two other adult males in this group had testes 9 × 5 and 11 × 5 mm, respectively, on 13 April. The data thus suggest that in mid-April 1968 in Campeche, males were coming into breeding condition and that females were on the verge of doing so. This may account for the fact that the groups usually encountered were of breeding flock size, i.e., fewer than 10 birds.

The probable proximity of the breeding season, given appropriate environmental stimuli, was further suggested by behavior of some adult birds from 16 to 18 April. In the woodland by Zoh Laguna, in that period, pairs

of adults away from the regular flock were seen several times. In Hardy's study of the captive flock of 6 Yucatan Jays from 1968 to 1972, the 2 oldest birds (a male and a female), especially at the time of onset of reproduction, showed a tendency to stay together away from other group members. In each year from 1969 to 1971, this was in April. Thus the pair behavior of the adults in the wild in mid-April 1968 is probably significant with respect to onset of breeding.

Breeding Flocks

Size, composition, number.—The social unit during the breeding season invariably was a flock; that is, birds in the breeding season were not members of simple male-female pairs but of groups of more than 2 adults and, usually, yearlings and 2-year-olds. Table 1 shows the sizes and makeup of the flocks regularly observed from the Xpujil-Zoh Laguna road in the breeding season in 1972 and 1973. Our field work was not at perfectly comparable times in the 2 years. June 1972 was a period primarily of laying and incubation in what were apparently the first nestings of the season, whereas in July 1973 the breeding season was well along, with fewer active nests and many nests having already fledged young. Thus, the largest of the 1973 flocks may have been composite groups, of the order of winter flocks (see beyond), formed by the amalgamation of 2 or more breeding flocks. Arguing for that interpretation is the fact that we recognized 10 distinct flocks in 1972 but only 9 in 1973. In our analysis of the size and composition of the breeding flocks we follow a conservative interpretation by assuming the 2 largest 1973 flocks to be atypical, perhaps composite, and therefore exclude them. On that assumption it may be seen in Table 1 that the flocks consisted of 4 to 15 individuals of adult phenotype; the mean was 6.4 per flock in 1972 and 8.7 in 1973, but differences between years were not significant ($p > .05$, Mann-Whitney U-test). A few flocks contained 2-year-old birds in 1972 but none was seen in 1973. Several flocks in 1972 contained 1 or 2 yearling birds; in 1973 all flocks contained at least 2 yearlings and 2 contained 6. The 1972 year-class was large relative to that of 1971, and the presence of additional yearlings in 1973 was largely responsible for the larger size of flocks in that year. The sizeable number of juveniles already fledged in July 1973 indicated that that year-class potentially was also relatively large.

Members of at least some discrete flocks apparently had more than 1 nest. In 1972 nests 1, 11, and 12 all seemed to be within the range of a single flock, as did nests 5, 8, and 9 (Table 1). All 3 nests in each group were close together, well within the normal radius of movements of flocks in the breeding season (see subsequent section on flock movements), and we could detect no dividing lines between them in the movements of birds. Nests 5, 8, and

TABLE 1

COMPOSITION OF BREEDING SEASON FLOCKS OF YUCATAN JAYS NEAR XPUJIL, CAMPECHE, 1972, 1973

Flock Location[1]	Number of: Adults	2-year-olds	Yearlings	Juveniles	Total Birds
1972					
Nests, 1, 11, 12	10	3	0	0	13
Nest 2	5	0	1	0	7[2]
Nest 3	4	0	0	0	4
Nest 4	9	0	0	0	9
Nests 5, 8, 9	6	0	2	0	8
Nest 6	7	1	2	0	10
Nest 7	6	1	0	0	7
Nest 10	5	0	1	0	6
0.5 km	6	0	0	0	6
2.4 km	6	1	0	0	7
TOTAL	64	6	6	0	77
1973					
0.8 km	6	0	2	4	12
Nest 1	6	0	6	8	20
3.9 km	9	0	4	4	17
Nest 4	10	0	2	5	30[2]
Nest 9	5	0	2	2	9
6.9 km	15	0	4	5	24
Nest 8[3]	28	0	3	11	42
7.8 km[4]	24	0	3	5	32
8.6 km	10	0	6	4	20
TOTAL	113	0	32	48	206

[1] Locations of flocks given either as the nest site(s) of the flock or as road km north of Xpujil.
[2] Total flock size known but ages of some individuals unknown.
[3] "Flock B."
[4] "Flock C."

9 were active simultaneously, and separate small groups of birds seemed involved in activities of incubating and feeding young at them. Other interpretations are possible, but the observations seem to suggest that the situation involved division of labor within 1 communal flock with 3 concurrent nests. In the other group, nests 1 and 12 were at about the same stage; nest 11 was a later effort, built after the other 2 had reached the nestling stage. Otherwise, the situation appeared similar to that with nests 5, 8, and 9. In 1973 the presence of fledged juveniles in the flocks tending nests 1, 4, and 8 (Table 1) seemed strong evidence that members of at least those flocks

nested more than once. The large numbers of such juveniles in the vicinity of nests 1 and 8 suggest the possibility of more than 2 nests by those groups. We cannot say how much overlap in time there was between these putative multiple nestings in 1973, but clearly overlap was little since juveniles from early nestings tended nestlings of later ones.

Distribution and movements.—The flocks were unevenly distributed along the study transect in both years. Each year there were 4 flocks along the northern ⅓ of the road where there was the most varied mixture of milpas and forest. The southern ⅓, near Xpujil, where milpa clearings are also common, contained 4 flocks in 1972 but only 2 in 1973. The middle ⅓ of the transect, where milpas are uncommon and unbroken forest the rule, contained only 2 flocks in 1972 but 3 in 1973. The ranges of all flocks included either small clearings along the road or isolated milpas. From this pattern and from observations elsewhere in Campeche and Quintana Roo, it appears that the breeding flocks prefer forest edge and that optimal habitat is a mixture of clearings and patches of forest.

Important questions concerning the ecology of the social system of these birds center around territoriality or home range. Two major difficulties hampered our study of the use of area by the flocks. While they were in the forest they were usually impossible to follow. The second problem was the difficulty in capturing birds alive for color-marking. Too few were marked late in June 1972 to be of much help in the study of flock movements in that year. In many instances it was impossible to be confident of the identity of a given flock, especially near boundaries of ranges of 2 flocks. The greater, but still modest, trapping success in January 1973 provided a group of marked individuals that were of considerable assistance in ascertaining the movements of 2 flocks; 1, which we called flock B, "owned" nest 8 and contained 2 marked birds; the other, flock C, was located north of the other, centering at 7.8 km N Xpujil, and contained 4 marked birds. Locations of members of these flocks and some of their prominent movements are shown in Fig. 2. The 2 flocks appeared to occupy ranges roughly comparable in size; in both cases the maximum distance between sightings was about 400 m. Both were highly mobile within their range, moving distances on the order of 100–200 m and then back in the opposite direction within a few minutes. Both flocks were extraordinarily large (Table 1); as suggested earlier they perhaps were comprised of more than 1 breeding flock. It is possible that their ranges were larger than those of smaller flocks, but they did not appear to behave differently from known simple breeding flocks. At times they moved as tight, complete groups, especially at dusk. At other times they were spread out in looser units; occasionally the flocks were fragmented into small somewhat independent sub-flocks.

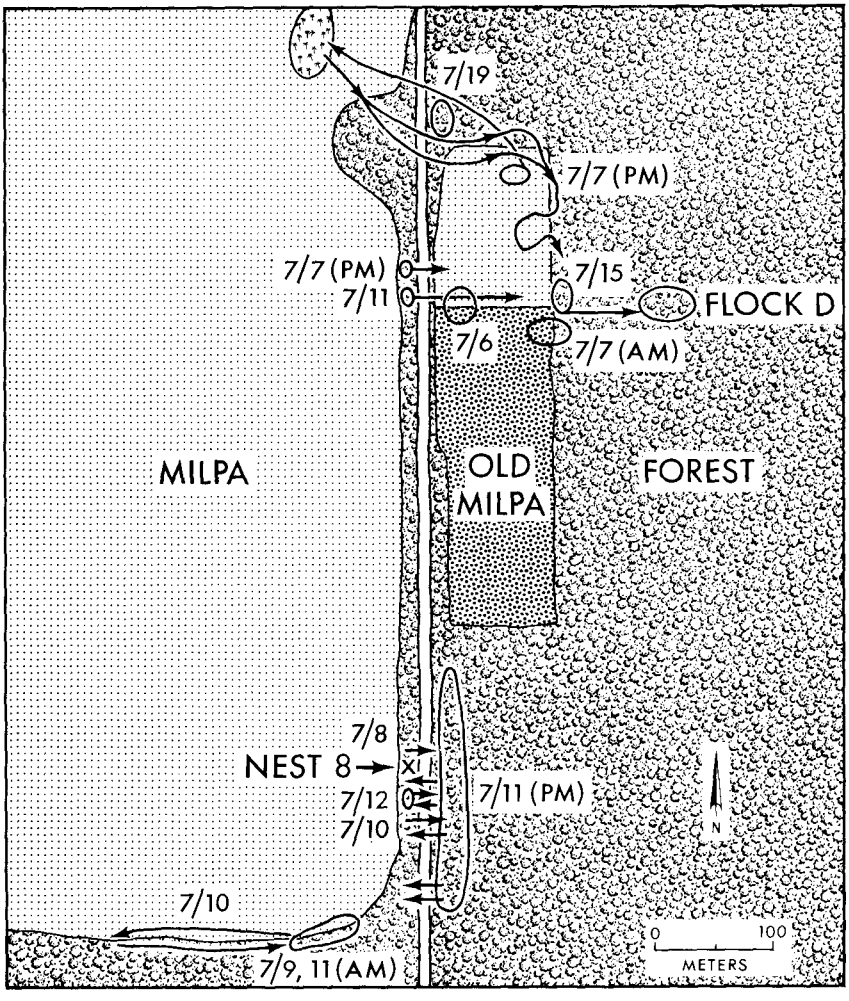

FIG. 2. Map of a portion of study area showing dates and locations of sightings of Yucatan Jay flock B (at southern edge) and flock C (at northern edge), and location of single sighting of flock D, all in July 1973. Lines with arrows indicate movements. Different patterned area at northern edge visited by flock C on 7 and 19 July was site of cluster of small papaya trees.

The 2 flocks apparently did not interact. The shortest distance between observed locations of the 2 was approximately 300 m. A possible third flock (flock D, Fig. 2) approached and overlapped the range of flock C. We followed this group of about 20 birds about 100 m east into the forest from

the eastern edge of the milpa where flock C was frequently observed. We observed the birds at close range as they approached us in the forest in response to broadcast of recorded calls but saw no marked individuals. Because of the absence of marked birds, 1 or more of which were conspicious on nearly all observations of flock C, we believed this group to constitute a separate flock. We never saw interactions that would indicate interflock hostility.

In summary, our observations of flocks B and C indicate that each flock occupies a separate home range within which the flocks or segments thereof are at times highly mobile. The size of this area ranges up to 400 m in diameter. Much foraging and other activity appears to take place at or near forest-field edges. Observations of other flocks in both years are consistent with the above summary. Whether the group ranges are territories defended against other flocks is unknown. The dispersion of flocks in both years, at intervals of several hundred meters along the road, in a transect of what appeared to be continuous favorable habitat, suggests that some spacing mechanism exists. If this mechanism is territorial-type aggression between flocks, it probably occurs in the spring when large winter flocks split into the smaller breeding units; it seems absent among the usually well-separated breeding flocks.

Social behavior.—Yucatan Jays within both breeding and nonbreeding flocks engage in ritualized displays and postures, as described by Hardy (1974b). The most common of these are "Up-fluffing" and "Peck-preening," the typical action and reaction of 2 or 3 closely spaced individuals. This behavior serves in greeting and appeasement; fighting is rare, as are threat and more extreme appeasement in response to aggression. The rarity of such behavior is probably due to the development of the "Up-fluffing-Peck-preening" ritual, and allofeeding.

In the wild Up-fluffing and Peck-preening were a prominent feature of group behavior when the flock had paused to rest when foraging or when the birds were sunning or preening in early morning hours in the top of a tall tree or after a rain. Among Hardy's captives such activity was not clearly correlated with sex, age, or social dominance. The 2-year-old in the color plate is beginning the Up-fluffing display.

Social feeding of one bird by another was less common but still frequently observed. It appeared that any individual of any age class might pass food to any other bird. Often food was passed back and forth or through the bills of several birds before being eaten.

We recorded no instances of fighting in the wild; in captives Hardy induced overt aggression by removing a bird from a flock for several days and then reintroducing it. In the few minutes after this reintroduction, the newly

arrived individual was chased and pecked on the tarsi and head. It responded by extreme appeasement gaping. Such treatment ceased within a few minutes. Hardy's unpublished data on the closely related San Blas Jay, of which he had many more captives from different family groups and different locations, show that the reaction of a communal group to a stranger is the same as just described, but that it continues and the new individual is never accepted, and is sometimes injured or killed. Spontaneous occurrences of such activity were extremely uncommon in the Yucatan Jay and seen not more than 5 or 6 times between 1968 and 1972 in the captive flock. Our failure to see fighting in the wild probably indicates that individuals rarely if ever become separated from the flock for sufficient time to invoke the reentry pecking and chasing behavior.

Nests and Nest-building

Nearly all of the active nests found were within 5 m of the edge of the forest. Two were deeper into the forest and one was in one of a narrow row of trees isolated from the forest itself. Of course, edge nests are easier to find than others and there is thus bias in our sample, but it seemed unlikely that there were enough unknown nests deep in the forest to offset the apparent preponderance of ones at the edge.

Most nests were near the lower edge of the upper canopy, from 4.3 m to 9.1 m up (mean 6.2, N = 10). The top of the forest canopy was 2–5 m above the nests.

As with all species of *Cissilopha*, the nest was a flimsy platform with shallow cup and composed mostly of a collection of sticks inlaid with a few finer twigs or coarse plant fibers. The lining was never dense, often permitting the clutch or nestlings to be viewed from below. We noted no instances in which the nest failed to remain intact beyond fledging of the young.

Nest-building in the captive flock was preceded by a period in which the birds carried material around but dropped it or deposited it at the nest site without visible constructive effect. In 1969 the first carrying of material was observed in January when, before nest material was provided, the birds began pulling pine needles through the wire mesh of the outdoor aviary to carry them about. Hardy immediately provided sticks and coarse grasses, but this did not stimulate any increase in this earliest manifestation of building. Between 15 and 23 April there was a marked increase in the carrying of nest-building material. The adult male carried 1 stick around, placing it here and there in crevices, and the cage wire mesh. His mate also carried sticks and was observed presenting a stick to him. On 5 May nest-building actually began.

In this captive flock, the female (at least 4 years old) was principally

responsible for the nest in 1969 and 1971, but in the same flock in 1970 her mate (also at least 4 years old) seemed largely responsible for its construction. In 1969, the male carried many sticks to the nest but usually left them with the female, who built the nest. In 1970, the roles were reversed and the female seemed of less help to the male than he had been to her. Other birds in the flock (2 two-year-olds and 2 yearlings in 1969, that became 2 three-year-olds and 2 two-year-olds in 1970) made no constructive efforts toward the nest's construction, although each time in the early stages they were busy carrying about sticks, visiting and perching on the nest, pulling sticks from it, or moving them about. Rarely, they were chased from the nest by the building pair and usually they were ignored or "tolerated." Concerted nest-building in 1969 lasted from 5 May to 17 May. In 1970 the nest was completed in 1 week, 7–13 April.

We have information on building of only one nest in our field studies. A half-completed nest was found on 23 June 1972 (nest 11). At least 3 birds, 2 adults and one 2-year-old (with almost completely black bill and partial yellow eye-ring), were nest-builders. One of the adults and the 2-year-old brought nest material and sat in the nest. The other adult was seen carrying material but because none of the birds was color-marked we do not know that 2 adults actually built. This sub-flock included at least 2 adults, 2 two-year-olds, and 1 yearling. (The yearling as indicated in Table 1 was otherwise undetected in our studies of the whole flock in this part of the study area.) By 30 June an adult was sitting on the completed nest for protracted periods.

Eggs and Laying

Eggs of all 4 species of *Cissilopha* are colored similarly and are unlike those of other New World jays. The base color is mottled pale to medium pinkish-buff, speckled with reddish-buff.

We obtained no data on laying in the wild. In Hardy's captive flock the oldest female laid several clutches or parts thereof in 1969, 1970, and 1971. On 12 May 1971 she laid a first egg prior to 09:15. On each successive day through 15 May an additional egg was in the nest when checked before noon. Four eggs were probably the full clutch. This same female laid 2 eggs on successive days on several other occasions, but we have no other full record for a complete clutch.

Of 8 study area clutches, 6 were of 5 eggs and 1 each was of 4 and 6 eggs. Hardy (1976) reported a clutch size of 3 or 4 based upon limited data for both Bushy-crested and San Blas jays.

Incubation

We have data on incubation from 9 nests observed in 1972. Of 4047 min of observation 1110 min were at 1 nest. We concentrated on the activities of

TABLE 2

INCUBATION AND FEEDING OF INCUBATING YUCATAN JAYS

Nest	Minutes (days) of Observation	% of Time Clutch Covered	No. of Absences (With Guard)	No. of Feedings (By Yearlings)	Minimum No. of Feeders (Yearlings)
1	688(6)	96	3(3)	25(0)	2(0)
3	1110(8)	95	12(0)	20(0)	1(0)
5	450(5)	92	2(2)	7(0)	1(0)
6	435(3)	95	4(3)	10(0)	1(0)
7	30(1)	93	1(0)	2(0)	1(0)
8	465(3)	—	—	11(2)	2(1)
9	230(3)	100	0	1(0)	1(0)
Total	3408	95	22(8)	76(2)	

fully grown attendants at the nest. It appeared as if 1 bird did all of the incubating at each nest. Our evidence for this statement is all indirect, because of unmarked birds. We observed no instance of 1 bird replacing another in incubation, though on several occasions an incubating bird departed immediately after being fed by another bird which remained at or near the nest. All incubating birds were adults, and probably were females. On 19 April 1974 Jorge E. Orejuela collected an incubating adult female from a nest. In Hardy's captive flock practically all of the incubating was done by the adult female parent; the male parent once sat on the eggs briefly. If our surmise is correct that incubation is done nearly exclusively by the female parent, then *C. yucatanica* differs in this respect from *C. melanocyanea* and *C. sanblasiana nelsoni*, in which Hardy (1976) has shown that more than 1 individual incubates.

Data on attentiveness and feeding of the incubator are summarized in Table 2. Data from 2 nests are omitted because of the probability that the presence of the observer caused abnormal behavior. In nearly all of the observation periods at all nests, regardless of the stage, the incubating bird remained on the eggs for over 90% of the time. Absences of the sitter averaged 5.4 min; 10 of 22 absences were for less than 3 min and only 2 were for longer than 10. Often another bird was present near the nest, especially when the sitter was absent. These "guardian" birds usually remained silent and relatively motionless, perched from as close as the nest rim to 5 m away, but usually in the nest tree. At nest 3 guarding was never observed.

Sitting birds were fed at the nest by other birds at irregular intervals averaging about 45 min. Two of these feedings were by yellow-billed yearlings; the rest were by adults; 2-year-olds were not observed to bring food. We

know that at least 2 adults participated at nest 1 and at least 1 adult and 1 yearling at nest 8. Probably greater numbers participated, as we occasionally saw several birds near nests containing eggs. For example, on 21 June 1972 an adult that had just fed the sitter joined a group of 5 other adults in a tree 30 m from the nest; 4 members of the group were carrying food. At times the delivery of food to the incubator was preceded and/or accompanied by begging by that bird. Wings were spread and fluttered, tail and head were raised with open gape, and, in some instances, distinctive calls were given. This begging was more common at some nests than at others; it apparently did not increase in frequency with advancement of incubation as in *C. melanocyanea* (Hardy 1976). In no other obvious respect did feeding of the incubator differ between the Yucatan Jay and either the Bushy-crested or Nelson San Blas jays studied by Hardy.

We refrained from frequently disturbing incubation to check nest contents. As a consequence, we have little information on incubation periods or on losses of eggs. The incubation period of a clutch of eggs in captivity was 17 days and our field observations are consistent with such a period.

Hatching through Fledging

Hatching.—In 1972 the earliest date of hatching in one of the nests under study was 24 June; hatching was underway on that date in nests 4, 5, and 7, and within 2 days of 24 June in nests 3 and 6. Hatching occurred on 30 June in nest 1. That few if any successful clutches hatched appreciably earlier than late June in that year is indicated by our failure to observe any fledged juveniles before our departure on 1 July. By contrast, Orejuela observed young being fed in a nest as early as 22 May in 1973, and fledged white juveniles were common in that year on 4 July when we arrived at the study area. Those juveniles must have hatched at least by early June.

Hatching within a clutch must be nearly synchronous. The week-old nestlings collected from 2 nests in 1972 closely resembled their nestmates in size and stage of development except for a "runt" that fell out of one nest about 5 days after hatching.

Brooding and nest sanitation.—Immediately after hatching the young were brooded almost continuously. The percentage of time devoted to brooding declined gradually during the first half of the nestling period. This pattern is best illustrated by the percentage of our observation periods during which young were brooded at nest 4 in 1973, as follows: day 0 (day of hatching), 91% of 242 min; day 1, 83% of 498 min; day 2, 78% of 265 min; day 3, 83% of 295 min; day 4, 95% of 328 min; day 5, 87% of 172 min; day 6, 62% of 108 min; and day 7, 62% of 311 min. We have no data for the middle portion of the nestling period, but the percentage of brooding time

must decline rapidly, for no brooding was observed in the 9 days prior to fledging at nest 1 in 1973.

Usually when the brooding bird left the nest, it was replaced by another bird that remained at or near the nest. On several occasions at nest 4 (1973) the replacement settled on the nest as if brooding. In all instances birds that actually sat on nestlings were black-billed adults. Since such birds were not individually marked we know only that at least 2 adults participated in brooding.

Fecal sacs were removed from nests by adults, at times by the brooding bird, at times by others. Fecal sacs were either eaten quickly, or carried away; they were never dropped to the ground within view of an observer.

Attendant birds spent substantial amounts of time in caring for the nest. Often a bird appeared to closely examine the undersurface of the nest, occasionally picking at it and probing into it with its bill; this behavior gave rise to our shorthand term "inspecting." Less often a bird spent 20–30 min scanning the entire nest, pecking at or into it frequently, apparently consuming small items. These were presumably larvae of a fly (*Mydaea* sp., Muscidae) that parasitizes nestlings; most nestlings examined had several subcutaneous cysts containing these larvae. Only adults performed this behavior and there probably was a division of labor among attending adults. A green-tagged adult at nest 1 (1973) fed nestlings but apparently did not participate in nest care. We seldom saw a bird alternate directly between brooding and inspecting. Inspecting was seen only after hatching and it seemed to be more common in more advanced nests, which lends credence to the hypothesis that nestling parasites are involved in it. Hardy (1975) reported similar behavior by Bushy-crested, San Blas, and Mexican jays. So much time (approximately 60% of one 30 min observation period) is devoted by Yucatan Jays to this form of nest care that it must be important to nest success.

Feeding of nestlings.—Data on frequency of feeding of nestlings and on the number and ages of feeders are given in Table 3. Feeding rates accelerated as the nestling period advanced.

At all of the nests but 2 it was certain that more than 2 birds participated in feeding. We were unable in most cases to recognize individuals, so the numbers of feeders may have been considerably higher than those listed in Table 3. It is, however, clear that feeding of the nestlings in the Yucatan Jay is, in at least a limited sense, a communal effort. In respect to communality *C. yucatanica* resembles its close relatives *C. melanocyanea* and *C. sanblasiana* (Hardy 1976) and other New World jays such as *Aphelocoma ultramarina* (Brown 1970, 1972) and *A. c. coerulescens* (Woolfenden 1975). (Detailed comparisons among these species will be discussed below.)

TABLE 3

FEEDING OF NESTLING YUCATAN JAYS

Nest	Days	Min Obs.	Min per feeding	Total feedings	No. of Feedings by:[1] Adults	1-yr. olds	Juvs.	No. of Feeders Adults	1-yr. olds	Juvs.
1972										
4	4	484	54	9	9	0	0	3	0	0
5	3	590	37	16	16	0	0	2	0	0
9	1	180	45	4	4	0	0	1	0	0
Totals		1254	43	29	29	0	0			
1973										
1	9	2181	15	141	138	3	0	3	2	0
4	10	2832	20	142	131	5	6	3	3	2
8	3	327	33	10	9	1	0	3	1	0
Totals		5340	18	293	278	9	6			
Grand Totals		6594	20	322	307	9	6			

[1] No. 2-year-olds fed nestlings.

The 2-year-old age group is the only one for which we have no evidence of feeding of nestlings. The lack of data in this case is almost certainly a sampling error, a result of the scarcity of birds of this age in both years of our study (see Table 1). Even though birds of all ages probably participated in feeding, it is nevertheless clear that birds of adult age contributed most of the food. Data on 2 marked birds give conflicting indications of the division of the labor of feeding nestlings among adults. At nest 5, 1972, the marked adult, "Orange," made 15 of the 16 feeding visits recorded; the other feeding was by an adult that spent most of the period brooding the nestlings. "Green," the marked adult at nest 1, 1973, fed nestlings 27 times after it was marked. In that same period we recorded 56 additional feedings, of which adults contributed 55. We know that there were (at least) 2 feeding adults in addition to "Green." It appeared that the division of labor at nest 1 was more nearly equal than at nest 5. This difference may have been related to the different stages of the 2 nests; the observations at nest 1 were made in the last few days of the nestling period, with no brooding, while those at nest 5 were in the initial days, with brooding during a high percentage of time. For the Bushy-crested Jay, Hardy (1976) found 8 adults feeding nestlings at 1 nest, with numbers of visits per individual as follows: 38, 22, 22,

17, 12, 10, 8, and 2. At a nest of the San Blas Jay, Hardy observed the following numbers of visits per respective adult feeder: 63, 61, 50, 26, and 6. Large numbers of birds (as many as 16) fed young in the nests of the Mexican Jay studied by Brown (1972); birds older than 1 year did a large percentage of the feeding; the visits otherwise were divided according to no obvious pattern.

The manner of delivery of food varied at nests in early stages of the nestling period. When a feeder arrived at a nest with a brooder present it often delivered food to the brooder, which then fed the young. When another bird was present but not brooding, it likewise often acted as an intermediary. At other times the bearer of food fed the young directly or delivered some of its food to the other bird before both of them fed the nestlings. Even white-feathered, fledged young-of-the-year acted as intermediaries in feeding nestlings. On 21 July 1973 at 17:10 three juveniles came to nest 4; 5 min later a 4th came and fed the adult brooder, which in turn fed the nestlings; 4 min later another adult came to the nest, fed 1 of the fledged juveniles, which then fed another juvenile; the latter delivered food to the brooder and then both fed the nestlings!

Many visits were made to nests with nestlings without the delivery of food. The nest with nestlings often appeared to be a focus of activity by the flock. At 09:50 on 19 July 1973 an adult arrived at nest 4 and delivered food via the brooder; it then began inspecting the bottom of the nest; 5 min later the 2 adults on the nest were joined by a 3rd and a group of 10–15 adults, 2 yearlings, and 3 juveniles; all came within 1 m of the nest; after about 10 min all but 2 adults left.

Fledging and post-fledging care.—We have no field data on length of the nestling period. A male Yucatan and female Nelson San Blas jay that paired in captivity reared 1 nestling to age 26 days, at which time the nestling seemed grown and feathered to a stage comparable to fledgings we observed in the field. We did observe the final days of activity at 2 nests in 1973. On the morning of 9 July (the 6th day of intensive observation) the 2 surviving young of nest 1 remained in the nest as usual. In the afternoon they climbed out of the nest onto supporting limbs, venturing as far as .5 m, but they returned both times. The next day they behaved similarly, but by 17:34 both were out of the nest, perched in different locations, each about .5 m from the nest. On 11 July they were in similar positions at 06:10. Later in the morning they became increasingly active, moving from limb to limb, farther away from the nest; one returned to the nest at 06:46 and departed again at 07:26, after which we saw neither in the nest again. By 12 July they were heard begging loudly about 30 m away but were mobile enough to evade our search and we did not see them again to recognize them. Similar events

occurred at nest 9, which we discovered on 5 July just as the 2 young had apparently begun to fledge.

Throughout the period of field work in 1973, when the strikingly white-feathered juveniles were much in evidence, we frequently saw and heard them begging and being fed by other members of their flocks. Much of their food in the initial weeks following fledging must have been provided by older birds, even though juveniles soon reach full size and can move with the flock.

Nest Losses and Breeding Success

All but 2 of the 16 nests whose histories we followed at all in either year suffered losses of either eggs or nestlings, or both. Five nests were complete losses; 4 had contained eggs and 1 had nestlings before being found empty and abandoned. At the most advanced stage for which we obtained data, 8 nests contained nestlings. Numbers of nestlings per nest were as follows: 4, 4, 3, 2, 2, 1, 1, and 1. Comparison of these numbers with the most common clutch size of 5 further indicates the magnitude and commonness of losses. Assuming that all 16 nests originally contained 5 eggs (a reasonable assumption) and that all of the nests suffered no losses after our most advanced observation (a very optimistic assumption), then 80 eggs laid gave rise to 33 fledged young, a success rate of 41% or 2.1 young fledged per nesting attempt. These figures are indices of maximal success. It is likely that additional nests were preyed upon or otherwise lost after our last observations.

Predation was probably the predominate cause of the nest losses. Tree squirrels (*Sciurus*) were common in the forest. One was circumstantially implicated in the overnight disappearance of a set of young nestlings, having been seen in the nest tree on the previous day. Another squirrel appeared very close to a nest with a young being brooded. The brooding bird gave a social alarm call and within 2 sec another adult jay appeared and flew directly at the squirrel, striking it bodily and knocking it off the limb. The squirrel fell about 3 m before it regained its footing and fled; the attacking bird soon flew away. Two of 4 nestlings in another nest were killed by a snake in spite of the prompt arrival of an adult jay, that pecked vigorously at it and called loudly. The 2 remaining nestlings fledged 5 days later. The preceding accounts indicate the sort of predation to which the jay nest contents were subjected; they also indicate that nest attendants defend the contents, with some success. Predation was not the only cause of nest losses; on 29 June 1972 one of the 4 5-day-old nestlings in nest 4 was helplessly hanging by its neck from the vegetation, apparently ignored by the other jays. We retrieved and kept it alive for a few days; it proved to have been the runt of the brood —which, incidentally, had earlier been reduced from 5 to 4 by unknown cause.

The overall breeding success rates calculated above appear to be rather low, especially as the estimates are conservative on the optimistic side. Yet the numbers of yearlings (32) and of fledged juveniles (48) in the population in July 1973 indicate that the reproductive effort in both 1972 and 1973 was moderately successful (Table 1). Assuming that the population studied included 10–12 breeding flocks, then in 1972 the breeding effort produced at least 2.7–3.2 young per flock. Similarly, in 1973 each flock had fledged, on the average, 4–5 juveniles even before the breeding season had ended. It is apparent from the discrepancy between the nest-specific success rate and the flock-specific success rates that flocks must have made multiple nesting attempts. As has already been described, and as is indicated in Table 1, we know that members of 2 different flocks each made at least 3 nesting attempts in 1972.

The few yearlings in June 1972 (Table 1) suggests low breeding success in 1971. This may have been related to lack of rain. Rainfall in the early months of 1971 was minimal. The 9-year mean cumulative rainfall at the Zoh Laguna station for January–May was 274 mm, whereas the total for those months in 1971 was 78 mm. The severe defoliation of the forest under these dry conditions probably results in lowered insect populations. Nesting in bare trees would increase susceptibility to predator detection; lowered food supply should also lead to increased mortality of young and perhaps to reduction in breeding attempts.

Winter Flocks

The social order in winter was very large flocks. Our information on these flocks is based on a brief study, 7–12 January 1973. In that period we concentrated on netting and marking birds and on determining locations, sizes, and composition of flocks. Although the high mobility of the flocks and the usual shyness of the birds made study difficult, it was clear that they were grouped into a small number of large flocks. There were at least 3 of these in the study area, and we obtained counts of 45, 45, and 53 birds in what we were almost certain were distinct groups. Another count of 51 was made of 1 of these, but we were uncertain as to which flock it was. These counts represented the minimum sizes of the respective flocks. We were unable to make accurate counts of the 3 age classes within these groups. We estimated that roughly 40–50% of each was composed of first-year birds. Of 9 birds netted, 4 were adults, 3 were first-year, and 2 were second-year birds.

As in the breeding season, the birds were concentrated in the vicinity of the northern ⅓ of the Xpujil-Zoh Laguna road (2 flocks, at least), with a secondary concentration (1 flock) near the southern end. The high mobility

of the flocks is attested to by the number and distribution of sightings and by direct observation of movements. Virtually all groups seen were on the move; we watched 1 flock of at least 53 birds move about 500 m from within the forest, across the road, and across a large milpa, in perhaps 20–30 min. At times over 50 m separated the vanguard from stragglers. Portions of the group stopped to forage briefly on or near the ground while others moved ahead. Another group flushed from a milpa near the road as our vehicle approached, flew across the road into the forest, then moved south through the forest, recrossed into the milpa, and moved out of sight deep into it, all within 15–20 min. Maximum distances between sightings of what we felt confident were the same flocks were on the order of 1 km.

We could not determine how cohesive these winter flocks were. It seems likely that they were formed by the simple joining together of neighboring breeding flocks. Observations the following July seem to suggest this, as described in the section on breeding flocks. Subsequently, at or prior to the onset of the breeding season, the flocks might well have resegregated. Unfortunately we have few data on the important question of whether the integrity of the breeding flocks was maintained between breeding seasons. Most of the birds marked in either June 1972 or January 1973 that were observed in a subsequent season had remained within the range of a single winter flock, but there were 2 exceptional birds. One was marked in June and was glimpsed briefly the following January at a point about 7 km from the point of capture: it was in the winter flock most distant from the bird's breeding season locality. One of the birds marked in January was repeatedly seen with flock C in the following July; the range of flock C was within the range of a different winter flock and other marked birds in flock C had been captured at a January station, over 1 km north of where the bird in question was captured. The movement of those 2 birds across ranges of other flocks raises questions crucial to the understanding of seasonal and annual changes in social organization; answers to these questions must await further study.

FOOD AND FORAGING

Information on the diet of the jays was obtained from direct observation of birds foraging and carrying food and from the analysis of the contents of 29 stomachs. Of these, 9 were collected in April 1968, 3 in June 1972, and 17 in the spring of 1974. Apart from rocks and soil, contents were about equally divided between plant and animal material. Seeds accounted for at least 68% by volume of the vegetable material; corn was the most important, occurring in 12 of the stomachs and comprising more than 43% of the volume of vegetable material. Arthropods were the primary animal food. Beetles (Coleoptera) were most common, occurring in 13 stomachs and ac-

counting for 19% of the volume of animal food. Families identified included Scarabeidae, Elateridae, Carabidae, Chrysomelidae, and Curculionidae, in roughly decreasing order of importance. Orthopterans were also important among animal items, occurring in 8 of 29 stomachs and having a volume of 30% of the animal material. Lepidopteran larvae were found in only 3 stomachs but comprised 17% of the volume of animal food. Spiders, ants, dipterans, and a mollusk (slug) were also found among the contents. Rocks and soil accounted for about 22% of the total volume of contents. In several stomachs the soil was inseparably mixed with material of animal origin, perhaps of soft-bodied forms such as earthworms.

The above sample of stomach contents is biased in its emphasis on the spring season. Our field observations to a degree remedy that bias as regards summer foods. In June 1972, caterpillars of several species (and perhaps of more than 1 family) were very abundant, mainly on the vegetation. In all but 1 of the several instances when we were able to identify food being delivered to incubating birds or nestlings in 1972, the items were caterpillars. Caterpillars comprised 40 and 60%, respectively of the contents of 2 of the 3 stomachs collected in that period. Corn was probably not important, as there was little in the stomachs or milpas, but berries were once fed to an incubating bird, and stomachs contained small seeds that probably were from berries.

In July 1973 caterpillars were uncommon and we had no evidence of their being eaten. On the other hand, fruit was abundant. We especially noted the abundance of a kind of berry, of about the size, shape, and color of coffee berries. Jays were seen a number of times eating them and bringing them to nests. On 4 occasions birds brought these berries to nests with nestlings, but each time they failed to deliver them to the young. Other types of fruit were also eaten in that period. On 2 dates, members of the large flock C (Fig. 2) made numerous trips to a milpa containing a clump of small papaya trees (escapes?) and brought back small (2–4 cm in diameter), green fruits. A member of another flock was seen in a forest tree extracting material from a larger ($5 \pm$ cm), brown fruit.

This analysis presents a picture of a population of omnivorous, opportunistic birds. Their diet was variable from season to season and from year to year, with a wide range of items even within a season. Apparently they were able to capitalize upon temporary, and perhaps spatially localized, abundance of items as different as caterpillars and berries.

Foraging behavior by birds with such a variable diet was found to be variable and generalized. Obviously much of their food came from or near the ground. We frequently saw birds fly to low positions, apparently to forage, and flushed birds from such positions, but their shyness and the

vegetative cover precluded actual observation of their foraging. In 1968, 1973, and 1974, jays were observed to forage at swarms of army ants (Hardy 1974a). From perches about 1–5 m above the columns of ants they appeared to capture invertebrates flushed by the ants. Other observations of foraging were primarily of jays in arboreal situations. Usually they moved along near the forest edge in loose groups, flying or hopping between perches, at various levels from the lowest strata to the top of the canopy. Most of the time they moved slowly and deliberately, examining foliage and branches of varied sizes, apparently thoroughly but not particularly systematically. In 1973, when fruit was so abundant, they concentrated on heavily laden trees and flew longer distances between bouts of foraging. Long flights to and from the small papayas were mentioned above and are illustrated in Fig. 2.

DISCUSSION

Control of Timing of Annual Cycle

Rain and resulting foliation may accelerate onset of reproduction, but nesting begins by May regardless of these factors, indicating an internal rhythm or photoperiodic control. Further evidence of this is provided by captive birds in California (in a rainfall regime exactly opposite that of Campeche) which began reproductive activities in April. On the other hand, in 1973 when little defoliation occurred at our study site, much successful fledging had resulted by June. In 1972, a dry year with 75% defoliation, no fledging had occurred by the end of June and all nests in early June contained eggs; no hatching occurred until late June.

Evolution of Communal Behavior

Comparison within Cissilopha.—We have demonstrated that the Yucatan Jay is social at all seasons and communally reproductive in groups of 4 to over 15 post-juvenal birds. The larger groups may have 2 or more simultaneous nests attended by separate units of the flock, and there seem to be 2 sequential or partially overlapping nesting phases in a breeding season. In all these respects the system is like that of Bushy-crested and Nelson San Blas jays (Hardy 1976). There are minor differences. In the Yucatan Jay only the putative parent female seems to incubate, while in the other forms incubation is by 2 birds. Attendants at a single nest were never known to include more than 6 post-juvenal birds in the Yucatan Jay, but in the Bushy-crested Jay at least 11 adults were known to feed young in 1 nest. There are suggestions of other differences as regards number and sex of participants in incubation and brooding, but these remain to be verified. (Certainly 2 birds incubate and 2 females brood in both the Bushy-crested and San Blas jays.)

Environmental correlates of the communal habits.—Are there similar environmental factors shared by these 3 jays that could explain their similar social systems? Certainly rainfall regimes, seasonal fluctuations in food supply, and foliage structure and dynamics are not similar in their ranges. The remaining prominent factor that the species share is a proclivity for forest edge and disturbed forest. Hardy (1976) tentatively concluded that such disturbed habitats had prevailed in the ranges of the Yucatan and Nelson San Blas jays but that montane forest habitat of the Bushy-crested Jay might well have only recently been dissected. Further reflection leads us to suggest that edge might well have prevailed in all 3 places for thousands of years. It seems certain that accelerated clearing by man has caused the spread and increase of the Yucatan Jay and its relatives. In other words, the present-day association with disturbance may be a recent artifact, and the original habitat of the jays was limited but stable forest edge. This pattern would conform to Brown's (1974) postulate of stable, isolated habitats as favorable for the origin and evolution of communal breeding.

Communality and population characteristics.—Yucatan Jays are generally sedentary. Eight of 10 marked birds were not seen farther than 0.5 km from the place where they were marked. As pointed out previously, 1 bird was seen in winter 7 km south of the place where it was marked in the previous summer. Another bird, marked in winter, was seen over 1 km north the following summer, having traversed the home ranges of 2 communal flocks. More data are needed to determine the frequency of such long movements. In this study we have not demonstrated that kinship is involved in membership of communal groups, but the likelihood of this is certainly increased by the sedentary character of the birds.

Brown's (1974) list of kin-selection correlates includes 2 known features of Yucatan Jays "that reduce and formalize intra-flock conflict. . . ." These are well developed display (Up-fluffing/Peck-preening) and conspicuous age difference in soft parts and plumage. The latter is most strikingly seen in the snow-white head and body plumage of juveniles.

Brown (1974) hypothesizes that kinship promotes successful communality by permitting altruistic acts to retain selective advantage without invoking group selection. This advantage is a relatively K-selected one. The correlates of K-selection, according to Brown, are delayed maturity, low reproductive rate, low dispersal, non-migratory habits, occupation of stable versus transitional habitat, and density-dependent mortality. Delayed maturity in the Yucatan Jay is certain. Full adult phenotype is reached in the 4th year of life (Hardy 1973), and active reproductive status may be delayed even longer by age-related social dominance (Hardy and Raitt 1974). Reproductive rate, as discussed earlier, was generally low in this study. Low dispersal,

non-migratory habits, and habitat stability have already been discussed; though our data are few on these factors, they seem to provide no strong contradictions. The only mortality we detected was through predation of nests, and predation is usually considered to be density-dependent.

In summary, of the several correlates of K- and kin-selection listed by Brown we have no data on some and incomplete data on others. But all data that we have are consistent with the mode of evolution of communal reproduction he suggests.

SUMMARY

We studied communal behavior of the Yucatan Jay (*Cyanocorax yucatanica*) mainly in 1972–73 in Campeche, Mexico, mostly in a strip of dense forest and cultivated clearings along 9.5 km of an unpaved road. Nesting, flock age-composition, movements, behavior, foods, weights, gonadal condition, and age characteristics were studied. Study of a captive flock in California provided some information.

The climate of the study area is warm, humid tropical. A dry season from November through April and a rainy season from May through October are irregular in onset and severity, effecting irregularity in foliation and defoliation.

Pre-breeding (April 1968) flocks of fewer than 10 individuals, moved about in discrete areas with some separation of pairs. Gonadal development suggested (as was experimentally supported) that due to internal rhythm or photoperiod, prior to rains, birds (especially males) were coming into breeding condition. Breeding was early in 1973 relative to 1972.

The typical reproductive unit consists of a pair of adults plus other adults, 2-year-olds, and yearlings. Breeding season flocks averaged 7.7 in 1972, 12.4 in 1973.

Some flocks had 2 or probably 3 overlapping nests per breeding season, with division of labor among flock members, including juveniles.

Breeding season flocks seemed to occupy separate areas, up to 400 m in diameter, with preference for patchy environments of forest and milpa. Dispersion of flocks suggested a spacing mechanism such as territoriality. Intraflock behavior was usually benign, even among captives, consisting primarily of ritualized displays, postures, and social allofeeding.

The flimsy twig nests seemed concentrated near the road, generally were 2–5 m beneath the crown of the upper canopy, and ranged in height from 4.3 to 9.0 m. Nest-building is communal but primarily by an adult male or female.

Eggs in all *Cissilopha* are pinkish-buff speckled with reddish-buff. Seemingly the clutch of 4–6 eggs was laid and incubated by 1 female, who spent over 90% of her time on the nest; she was fed there by 2 or probably more other birds. Eggs are apparently laid at 1-day intervals and the incubation period is about 17 days. Hatching seemed synchronous.

Brooding of young was almost continuous at first (90%), dropping to 62% by day 7, and to none in late nestling stage. A brooder off the nest was usually replaced by a guard that perched on the rim and occasionally appeared to brood. Some attendant birds spent much time "inspecting" and probing with the beak at the nest's interstices.

At all but 2 nests it was certain that more than 2 adults fed the young. Adults brought most food; fledglings contributed the least but sometimes were conspicuous visitors. Young probably fledge in about 26 days.

Flying juveniles beg for food and probably are largely dependent for it on the communal flock. Enterprise and opportunism characterize this species' diet.

Maximum reproductive success of all nests studied based upon probable number of eggs laid to young fledged was 41% or 2.1 young fledged per nest. Predation was the likely predominant cause of losses. Jays defended against predators with some success. Although fledging rates appeared low, our census of the population suggested 2.7 to 3.2 young per flock in 1972 and 4 to 5 juveniles per flock midway through the breeding season in 1973. Discrepancy here we attribute to multiple nestings. Low breeding success seemingly occurred in 1971, with low rainfall in early months of the breeding season probably a factor.

Winter flocks consisted of 45 to 53 birds, with roughly 40–50% being first-year birds. Winter flocks ranged up to 1 km. Most birds marked in June 1972 or January 1973 were observed the next breeding season within the range of a single winter flock; only 2 birds moved across flock boundaries.

A preference for forest edge and disturbed forest is shared by all *Cissilopha* jays. Probably the now common Yucatan Jay, like its relatives, was rare and restricted to natural edge and clearings prior to man's appearance. Kinship of breeding flock members seems likely based on their sedentary character. The species has certain behavior and ontogenetic changes that reduce and formalize intra-flock conflict. Correlates of K-selection (that promote values of kin-selection and altruistic communality) shown by the Yucatan Jay are delayed maturity, low reproductive rate, low dispersal, and nonmigratory habits.

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