COLONIALITY IN THE YELLOW-RUMPED CACIQUE AS A DEFENSE AGAINST NEST PREDATORS

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ABSTRACT.—Individuals of the colonial Yellow-rumped Cacique (*Cacicus cela*) in Amazonian Peru can defend their nests against predators in three ways. First, by nesting on islands and around wasp nests, caciques are safe from arboreal mammals such as primates, which destroy many more-accessible colonies. Caimans and otters that live in lakes also protect island colonies from snakes, which are vulnerable when crossing open water. Second, by clustering nests together and mobbing as a group, caciques can deter many avian predators, which take spatially isolated nests in small colonies. The effectiveness of mobbing increases with group size, which in turn is correlated with colony size. Third, by mixing their enclosed, pouchlike nests with abandoned nests, caciques can hide their nests from some predators. Overall, nests in clusters on islands and around wasp nests suffer the least predation, largely because they are well protected against the cacique's major predators. Females switch colonies after losing nests to a predator, usually to sites that offer protection against that predator. By this mechanism, the best colony sites accumulate the largest numbers of nests. It is unclear, however, why all females do not nest in the safest colony sites. I argue that nest predation favors coloniality because of the scarcity of nest sites that are safe from mammals and the increased effectiveness of group defense. *Received 15 June 1984, accepted 30 November 1984.*

PREDATORS can select for colonial nesting when (1) there is intraspecific competition for predator-free habitat (e.g. weavers: Crook 1964, seabirds: Lack 1968, blackbirds: Orians 1961, swallows: Snapp 1976, orioles: Pleasants 1979), (2) increased numbers are correlated with increased efficiency of group defense (e.g. gulls: Kruuk 1964, Patterson 1965, Gotmark and Andersson 1984; terns: Lemmetyinen 1971, Veen 1977; blackbirds: Picman 1980; swallows: Hoogland and Sherman 1976), (3) synchrony results in predator satiation (e.g. gulls: Patterson 1965; terns: Veen 1977, Nisbet and Welton 1984; weavers: Elgood and Ward 1963; blackbirds: Robertson 1972), (4) larger numbers of animals are more efficient at detecting predators (e.g. swallows: Hoogland and Sherman 1976, Wilkinson and English-Loeb 1982), or (5) there is a decreased probability of predation on centrally placed nest sites, i.e. the selfish-herd phenomenon (e.g. penguins: Tenaza 1971, egrets: Siegfried 1972, gulls: Siegel-Causey and Hunt 1981). No one of these adaptations, however, is likely to protect a colonial species against all of its potential predators. For example, nesting on islands may protect seabirds against mammalian predators but not against avian predators (Lack 1968). Increased group defense may work well against avian predators and small diurnal mammals (gulls: Kruuk 1964), but it is usually ineffective in deterring large mammals, nocturnal snakes, and some large or socially attacking avian predators (Kruuk 1964, Horn 1968). Predator satiation and selfish herd effects may work against nonrecruitable predators such as snakes (e.g. weavers: Elgood and Ward 1963) and owls (e.g. tern colonies: Nisbet and Welton 1984), but not against large or recruitable predators such as foxes (e.g. gulls: Tinbergen 1952). Horn (1968) found that clumped, central nests of the Brewer's Blackbird (*Euphagus cyanocephalus*) were less vulnerable to avian predators (mostly gulls), but that these same nests were more vulnerable to mammalian predators such as coyotes.

Therefore, any colonial species that is attacked by a variety of different predators may have to deal with several selective pressures that favor different spatial distributions of nests within colonies. The pattern of nest distribution in an area at any one time may represent the best long-term solution to the problems of

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avoiding predation, as found by Kruuk (1964) and Patterson (1965) for Black-headed Gulls (*Larus ridibundus*). Long-term responses should be most frequent among species living in stable habitats (Buckley and Buckley 1980). Alternatively, nest dispersion may represent a short-term response to the current availability of safe colony sites or the recent predation history in an area, as found for birds nesting on tidal flats (Beer 1966, Burger and Shisler 1980, Burger 1982). Short-term responses should be most advantageous in unstable habitats (McNicholl 1975) or in environments with unpredictable predators.

I examined the ways in which coloniality in the Yellow-rumped Cacique (*Cacicus cela*) enhances protection against nest predators in an undisturbed site in Amazonian Peru. Caciques are an ideal species for this kind of study for several reasons. First, with the exception of snakes, most cacique nest predators are diurnal and therefore can be observed as they attack colonies. Second, caciques have a very long (7–8 month) breeding season during which females nest several times. This makes it possible to study the proximate causes of female colony choice within a breeding season. Third, cacique colonies are attacked by several different predators, including mammals, snakes, and birds, each of which require different defenses on the part of caciques.

STUDY AREA AND METHODS

The Yellow-rumped Cacique is widespread in the lowlands of Central and South America. In southeastern Peru, the site of this study, caciques (*C. c. cela*) inhabit a variety of wooded and forested habitats and are especially abundant near open areas such as small jungle towns, along rivers, and around oxbow lakes. Caciques are dietary generalists. Adults eat fruit, nectar, and a variety of arthropods that they catch in the outer foliage of canopy trees and vines (Feekes 1981, Robinson 1984). Nestlings in southeastern Peru are fed almost entirely arthropods (Robinson 1985). Individual caciques feed solitarily or, occasionally, in small flocks of 2–10 individuals during the breeding season. Females nest together in colonies of 2–250 nests (Robinson 1984), of which as many as 100 may be active at any one time. Colonies usually are located in trees or shrubs that are at least partially isolated from the surrounding forest (Skutch 1958, Haverschmidt 1968, Feekes 1981; see below). Females build enclosed pouchlike nests, incubate, and feed young alone, with no help from males. Males sing and dis-
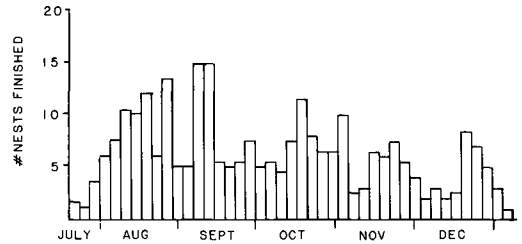

Fig. 1. The number of nests completed during 5-day intervals throughout the 1981 breeding season on Cocha Cashu.

play in colonies, and some help in mobbing predators (Feekes 1981, Robinson 1984).

Caciques nest from July through February (Fig. 1), a period encompassing the second half of the dry season (May–September) and the first half of the wet season (October–April; Terborgh 1983). There are usually from 40 to 100 active nests and from 2 to 6 active colony sites on Cocha Cashu at any one time. Most females renest at least once during the 8-month breeding season.

STUDY AREA

The study site was in the Manu National Park in the Department of Madre de Dios, southeastern Peru (71°19′W, 11°51′S; see Terborgh 1983 for a detailed description). All observations were made within a 4-km radius of the Cocha Cashu Biological Station, an area of undisturbed lowland flood plain forest of the Manu River. The remoteness of the site ensures that the community has a full complement of potential nest predators in what should be natural population densities. The forest around Cocha Cashu consists of various stages of riparian and lakebed succession.

Most caciques build nests along the margins of oxbow lakes. There are 12 such oxbow lakes, or cochas, between Cocha Cashu and the mouth of the Manu River. The study area included two lakes, Cocha Cashu and Cocha Totora, which form marshes along the lake margin that are invaded by shrubs including willows (*Salix* spp.), *Heliconia* thickets, and trees such as *Ficus trigona*, a fig, and *Heura crepitans* (Euphorbiaceae). Most cacique colonies are situated in these trees and shrubs. Three colonies were located in the forest at least 150 m away from the lake in isolated canopy trees.

PROCEDURE

I was present at Cocha Cashu for a total of 23 months (14 July to 26 October 1979, 12 August to 27 November 1980, 21 June 1981 to 7 January 1982, 20 June to 15 November 1982, and 2 August to 6 No-

vember 1983). Nearly all observations were made with binoculars from a boat. When watching a particular colony, I anchored the boat at least 25 m away to minimize disturbance. Some colonies were very high (30 m or more), and the birds did not appear to be aware of my presence.

Recognition of individuals.—Individual caciques were marked with distinctive colored leg-band combinations. Most caciques were caught in mist nests placed over the water near active colonies or roost sites. I ran nets on 303 mornings and 105 evenings. I captured and color-banded a total of 750 caciques and recaptured marked individuals 515 times. I have no evidence that the plastic leg bands had any adverse effect on caciques. In 1979 and 1980, only about 25% of the caciques on Cocha Cashu were marked, but by the middle of the 1981 season, over 90% of the breeding caciques on Cocha Cashu were color-banded. Therefore, I gathered the majority of data on individual movements between colonies in 1981, 1982, and 1983. Running nets near colonies had no appreciable effect on cacique nesting. Caciques usually returned to the colony within 2 h of their release.

Age determination.—From gradual accumulations of observations of individuals marked as fledglings, I found that cacique age can be determined reliably in their first and second years by plumage characteristics (Robinson 1984). First-year caciques have brown patches on the base of the bill and dark purple eyes. Second-year caciques have clear yellow bills and blue eyes, but males have olive edges on the belly feathers and females have traces of purple in their eyes and brown edgings on the head feathers. Adult males have black bellies and adult females have black heads.

Nesting phenology.—I visited each colony on Cocha Cashu daily and each colony on Cocha Totora at least once a week. For each nest I recorded which female was building it, the position relative to other nests, the dates of nest initiation and completion, dates on which incubation and nestling feeding began, and the dates on which young fledged or were preyed upon, or if the nest was abandoned. During the 5 yr of the study I followed the complete fates of 1,129 nests.

Predator attacks.—Whenever I observed a nest predator attack, I recorded the species, the colony it attacked, the size of the group of nests it attacked, which nests it raided, and the time it took to open each nest. I also described the techniques used to open each nest and recorded how caciques responded to the attack (left the colony, called, mobbed). When caciques mobbed, I recorded which individuals mobbed and which did not. I observed 87 nest predator attacks on cacique colonies.

Because some predators destroy all of the nests in any colony they attack (see below), the fate of each nest is not independent of those that surround it. For this reason, I used the proportion of colonies attacked by each predator for statistical comparisons of the vulnerability of different colony sites to each predator.

RESULTS

NEST PREDATORS OF THE YELLOW-RUMPED CACIQUE

There are three major classes of predators of cacique nests: mammals, birds, and snakes (Table 1). These predators can be divided into those that caciques mob [Black Caracara (*Daptrius ater*) and Cuvier's Toucan (*Ramphastos cuvieri*)] and those that they do not [all primates, Great Black-Hawk (*Buteogallus urubitinga*)]. Primates prey on all nests in a colony in one attack, while avian predators generally take only one or two nests per attack. However, some avian predators, and possibly some snakes, return to colonies where they have previously been successful. I have found snakes resting in or near colony trees between nocturnal attacks on active colonies, and Great Black-Hawks and Black Caracaras with individually recognizable plumages have been observed attacking the same colony on consecutive days. Each of these predators has distinctive methods of opening nests (Table 1), which made it possible to identify which predator preyed on a nest when I did not witness the actual attack. I assumed that any colony that was destroyed over a period of several nights by a predator that entered through the nest opening was attacked by a snake or a small mammal.

In spite of the diversity of nest predators, only 406 of the 1,129 cacique nests (36.0%) in the Cocha Cashu and Cocha Totora area were lost to predators, a relatively low figure for tropical birds (Oniki 1979) and low even for many temperate Icterinae [e.g. Red-winged Blackbird (*Agelaius phoeniceus*); Robertson 1972, Searcy 1979]. In the following sections I examine how colony site selection, the position and timing of nests within colonies, and colony switching by females protect caciques against their major nest predators.

COLONY SITE SELECTION

Protection against mammals.—Colony site selection is an adaptation that reduces vulnerability to mammals. Colonies surrounded by water (islands) or marsh vegetation (marsh trees) cannot be reached by primates or other

TABLE 1. Summary of the major features of attacks on cacique colonies by each of the major nest predators.

Nest predator	Number of attacks witnessed	Reaction of caciques	Number of nests taken per attack	Method used to search for and open nests
Mammals				
Brown capuchin (*Cebus apella*)	10	Call loudly; most leave colony	Whole colony	Reach through entrance of every nest within reach
White-fronted capuchin (*C. albifrons*)	2	Call loudly; most leave colony	Whole colony	Reach through entrance of every nest within reach
Squirrel monkey (*Saimiri sciureus*)	1	Call loudly; most leave colony	Whole colony	Chew small hole in bottom
Nocturnal mammal	0[a]	?	Whole colony	Chew small hole in bottom
Birds				
Great Black-Hawk (*Buteogallus urubitinga*)	10	Leave colony; mostly quiet	0–3	Shake nests, tear open nests with nestlings
Black Caracara (*Daptrius ater*)	22	Mob	0–1	Hang from nests, tear small (3–5 cm) hole in side near bottom; attack only active nests; take eggs and nestlings
Cuvier's Toucan (*Ramphastos cuvieri*)	32	Mob	0–2	Pull at nests with beak, tear long narrow hole in side near top; take eggs and nestlings
Snakes	0[b]	?	1–5	Attack several consecutive nights; enter through nest opening

[a] One colony destroyed at night.
[b] Two snakes found in colonies that were being abandoned at night.

arboreal mammals. For this reason, no nests were lost to arboreal mammals in any of these colonies (Table 2).

Polistine wasp-nest colonies also provide protection against mammals. In the Cocha Cashu area caciques cluster their nests within 2 m of the nests of two wasp species, *Stelopolybia fuscipennis* (4 colonies) and *Chartogis charterius* (identified from photographs, W. D. Hamilton pers. comm.). These wasps attack any large animal that approaches, including caciques. I have seen wasps repel attacks by white-fronted (*Cebus albifrons*) and brown (*C. apella*) capuchins and squirrel monkeys (*Saimiri sciureus*). Only nests situated very close to the wasps, however, are safe from predators. Twenty-four of 32 nests in one wasp-nest colony were taken by a troop of brown capuchins that approached the colony from underneath and reached into nests without disturbing the wasps. All 24 predated nests were at least 1 m from the wasp nest. The 8 surviving nests were less than 0.5 m above

the wasps. The wasps drove the capuchins away each time they tried to reach these nests. At least 2 other wasp-nest colonies were attacked by primates, but without success.

Edge-tree colonies occasionally were attacked by primates that crossed over the shrubby vegetation that connects these sites to the forest. However, only 4 of the 14 colonies were destroyed (Table 2), indicating that these colonies provide some protection from mammals, which seldom leave the forest to forage in lakebed trees and shrubs (Robinson pers. obs.).

Colonies on overhanging branches suffered the most intense mammalian predation (Table 2). Overhanging-branch colonies were significantly more likely to be attacked by mammals than island (Fisher exact test, $P = 0.022$), wasp-nest ($P = 0.040$), or marsh-tree ($P = 0.0004$) colonies. Overhanging-branch colonies also were attacked more often than edge-tree colonies, although the difference was not significant ($P = 0.054$). The high frequency of successful mam-

TABLE 2. Proportions of nests preyed on and number of colonies attacked by predators in different kinds of sites by different predators on Cocha Cashu, 1979–1983, and Cocha Totora, 1981–1983. All marsh-shrub colonies are on Cocha Totora. Edge trees are in figs isolated from the surrounding forest by low (<4-m tall) shrubby vegetation. Overhanging-branch colonies are on branches of canopy trees over the water. Marsh shrubs are completely surrounded by low (<2 m) marsh grasses. Sites are given in order of decreasing safety.

| Colony type | Number of nests[a] (number of colony years) | Proportion preyed upon (number of colonies attacked) | | | |
		Mammals	Snakes or mammals[b]	Birds	Total
Island	503 (5)	0.00 (0)	0.03 (1)	0.05 (4)	0.08
Wasp nest	125 (7)	0.21 (1)	0.06 (1)	0.09 (3)	0.35
Marsh shrub	138 (13)	0.00 (0)	0.57 (10)	0.04 (5)	0.61
Edge tree	230 (14)	0.20 (4)	0.07 (2)	0.27 (10)	0.54
Overhanging branch	133 (14)	0.65 (9)	0.12 (4)	0.11 (8)	0.88
Total	1,129 (66)	0.14 (14)	0.12 (18)	0.11 (30)	0.36

[a] Sum, over all years for the occupied colony sites of each type.
[b] Nocturnal attacks in which the predator entered through the opening at the top. Some nests may have been taken by an unidentified mammal.

mal attacks reflects the fact that mammals can reach colonies on overhanging branches without leaving the forest or crossing low vegetation.

Protection from snakes.—Colony sites also differed considerably in the frequency of presumed snake attacks and in the proportion of nests taken (Table 2). Colonies on islands are protected from snakes by the black caimans (*Melanosuchus niger*) that live in oxbow lakes in the Manu area. The only snake I saw swimming near the Cocha Cashu island colony was captured and eaten by a caiman that lived under the colony. The only snake that reached the island colony was captured and eaten by a giant otter (*Pteronura brasiliensis*). This snake reached the island during a severe flood, when the resident caimans were absent. Wasps apparently drive away some but not all snakes (N. G. Smith pers. comm.).

Marsh-tree nests appear to be especially vulnerable to snakes (Table 2). Nine of the 14 marsh-nest colonies were destroyed in a manner that suggested snake predation (see Table 1). Marsh-nest colonies were significantly more likely to be attacked by snakes than island (Fisher exact probability test, $P = 0.045$), wasp-nest ($P = 0.012$), edge-tree ($P = 0.0015$), or overhanging-branch ($P = 0.014$) colonies. The frequencies of presumed snake attacks did not differ significantly between colonies in other kinds of sites. Low colonies in marsh shrubs may be especially vulnerable to aquatic snakes

that live in marshes. When an island colony on Cocha Totora became connected to the rest of the marsh, the colony, which had contained over 100 nests the previous year, was abandoned.

Islands and wasp nests are the safest places to nest because they provide protection against both mammals and snakes. Island colonies were attacked by mammals and snakes significantly less often than colonies on overhanging branches (Table 2: Fisher exact probability test, $P < 0.001$) and marsh shrubs ($P = 0.004$). Similarly, marsh-nest colonies were significantly less likely to be attacked by mammals and snakes than colonies on overhangs ($P < 0.001$) and marsh shrubs ($P = 0.048$). Colonies situated in sites that can be easily reached by mammals (i.e. overhanging branches) and those that can be reached by snakes (i.e. marsh shrubs) have little chance of escaping predation. The differences in levels of avian predation among the different sites (Table 2) are related to colony size (discussed below).

Protection against birds.—Colony site selection by females also provides protection against avian predators, but for a different reason. Avian predators can reach any colony site (Table 2). The proportion of colonies attacked by birds did not differ significantly (Fisher exact probability test, $P > 0.05$) in any of the different kinds of colonies (Table 2). However, significantly more nests were taken by birds in edge-tree colonies than in all other colony types (χ^2

TABLE 3. Number of nests built each year in different kinds of colony sites on Cocha Cashu and Cocha Totora, 1979–1983.

Colony type	Number of sites	Years occupied	Nests[a]·yr⁻¹·site⁻¹ ($\bar{x} \pm$ SD)
Island	2	6	146.0 ± 74.4
Wasp nest	6	7	28.3 ± 15.8
Marsh shrub	13[b]	27	14.0 ± 8.1
Edge (fallen) tree (separated from forest by shrubby vegetation)	4	13	21.0 ± 13.0
Overhanging branches (of forest trees on edge of lake)	8	14	10.8 ± 7.2

[a] All counts made between 26 October and 15 November.
[b] All 13 colonies were on Cocha Totora.

test, $P < 0.01$). Similarly, significantly more nests were taken by birds on overhanging-branch colonies than on islands ($P < 0.01$).

These differences in levels of avian predation are largely a function of colony size. The colony sites that suffered the lowest overall levels of mammalian and snake predation (Table 2) tended to be selected by the largest number of females (Table 3). Island colonies, which suffered the lowest levels of predation, averaged more than twice as many nests as any other type of colony (Table 3). Wasp-nest colonies, which suffered intermediate levels of predation, were usually medium-sized (Table 3). Colonies on overhanging branches, in which 77% of nests were preyed on by mammals and snakes (Table 2), were significantly smaller than colonies in all other kinds of sites (Table 3: Mann-Whitney U-test, $P < 0.05$).

Large colonies are safe from Black Caracaras and Cuvier's Toucans because of the increased effectiveness of mobbing. Large groups of caciques were more effective at chasing away predators than small groups (Table 4). When toucans and caracaras tore at active nests, caciques dove at them and pecked them on the rumps. The more individuals that attacked these predators, the more likely the caciques were to drive them away before they had time to open a nest (Table 4). The number of caciques that mobbed predators was strongly correlated with colony size (Fig. 2), indicating that large colonies are less vulnerable to predation by toucans and caracaras. In fact, caracaras and toucans rarely attacked large colonies (Fig. 3). Most attacks were directed at small colonies (<13 nests), even though the majority of nests were found in large colonies (Fig. 3). Great Black-Hawks, which were not mobbed and could

reach any colony, attacked colonies in proportion to the number of nests in colonies of each size class (Fig. 3). Therefore, island and wasp-nest colonies suffered little avian predation (Table 2) because there usually were enough caciques present to chase away the two most frequent avian predators, the Black Caracara and Cuvier's Toucan (see Table 1).

POSITION AND TIMING OF NESTS

Clustering and local synchrony within colonies.— By nesting together in locally synchronous clusters within colonies, caciques can further reduce their vulnerability to avian predators. To measure the degree of clustering, I arbitrarily recognized two categories: "isolated" nests, defined as any nest or pair of nests separated from other active nests by at least 1 m; and "clustered" nests, defined as nests located within 1 m of at least 2 other nests. Clusters ranged from 3 to 76 nests that were densely packed together and often interwoven. One cluster consisted of 55 nests packed into a volume of about 2 m³. Because of the complex shape of these clusters, however, I was unable

TABLE 4. The effectiveness of mobbing vs. group size for attacks of Cuvier's Toucan and Black Caracara. Only data from caracaras and toucans that began tearing open nests are included. Values are means ± SE (sample size).

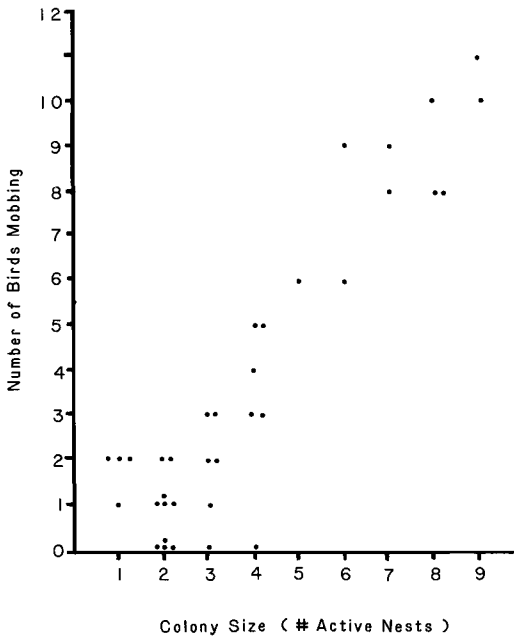| Predator is	Number of caciques mobbing predator
Successful at tearing open nest	2.2 ± 0.3 (23)
Chased away by caciques	5.3 ± 0.8 (20)
Mann-Whitney U-test, $Z = 3.12$, $P < 0.01$	

Fig. 2. The number of different individuals observed mobbing predators during attacks by Black Caracaras on colonies of different sizes (Spearman rank correlation, $r = 0.80, P < 0.001$). A bird was considered to be mobbing a predator if it flew at it or approached to within 0.5 m of the predator.
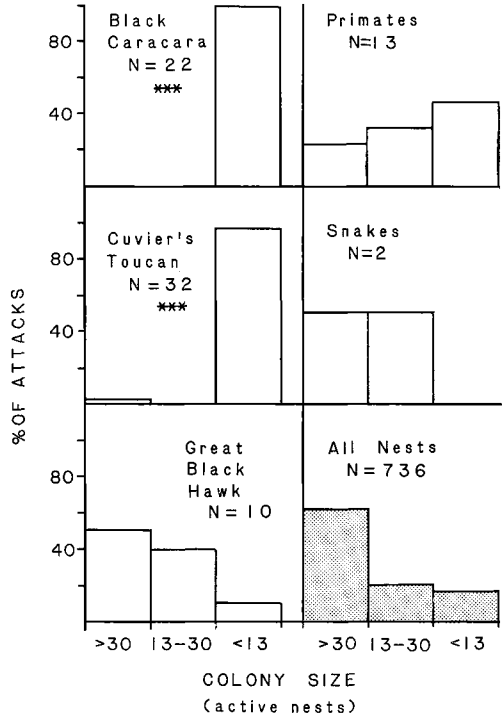

Fig. 3. Percentage of attacks witnessed on Cocha Cashu colonies of different sizes compared with the percentage of all nests in each colony-size category (shaded histogram). An attack is defined as an attempt to tear open or enter a cacique nest, whether or not the attack is successful. Snake attacks are inferred; they were not witnessed. In each case a snake was in the colony tree during a period when nests were being abandoned at night. N = number of attacks witnessed. *** = significantly different at the 0.001 level (χ^2 test, df = 2) from the percentage of all nests in colonies of different sizes.

to define "central" and "peripheral" nests within clusters. Small colonies usually consisted of a single cluster with a few outlying isolated nests. Large colonies had as many as 12 different clusters, with numerous isolated nests in between.

The timing and degree of synchrony within and between colonies was extremely variable (Fig. 4). Large colonies (e.g. colony 4 in Fig. 4) were active for long periods and were not particularly synchronous (SD of hatching dates = 38.9 days). In contrast, typical standard deviations of colonies of Temperate Zone birds range from 3 to 10 days (Emlen and DeMong 1975, Gochfeld 1980). Similarly, most clusters ("groups" in Fig. 4) were also relatively asynchronous, with nesting spread out over a long period (Fig. 4: SD = 33.5 days for group 7, 23.3 days for group 9, 47.9 days for group 5, 32.1 days for group 6). Because breeding was more or less continuous and most groups were small, I could not use any of the more widely accepted measures of synchrony to compare predation rates (see Gochfeld 1980). However, some

clusters did form in distinct waves, each of which was locally synchronous (e.g. groups 9 and 5 in Fig. 4). For this reason I examined the effects of local synchrony within clusters, rather than comparing predation vs. colony-wide synchrony.

I arbitrarily chose three categories of local synchrony within groups. "Highly synchronous" nests were those in which incubation began within ±5 days of at least 6 other nests in a 1-m radius. All of these nests were in very large clusters (20 or more nests). "Synchronous" nests were those in which incubation began within ±5 days of 2–5 other nests in a 1-m radius. This category included some less syn-
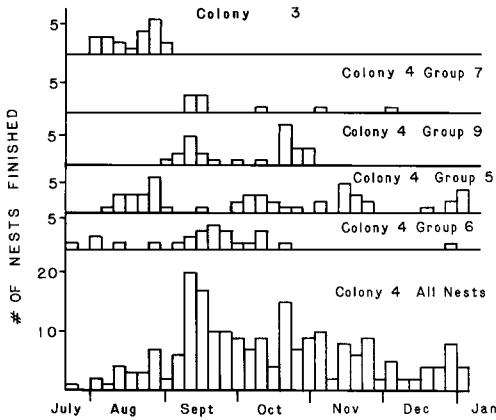
Fig. 4. Phenology of selected colonies and groups (clusters) within colonies on Cocha Cashu, 1981. A group is a cluster of ≥ 3 nests within 1 m of each other on the same branch of a colony tree. Colony 3 was on an edge tree; colony 4 was on an island. Number of nests finished refers to nests in which incubation was begun during each 5-day interval.
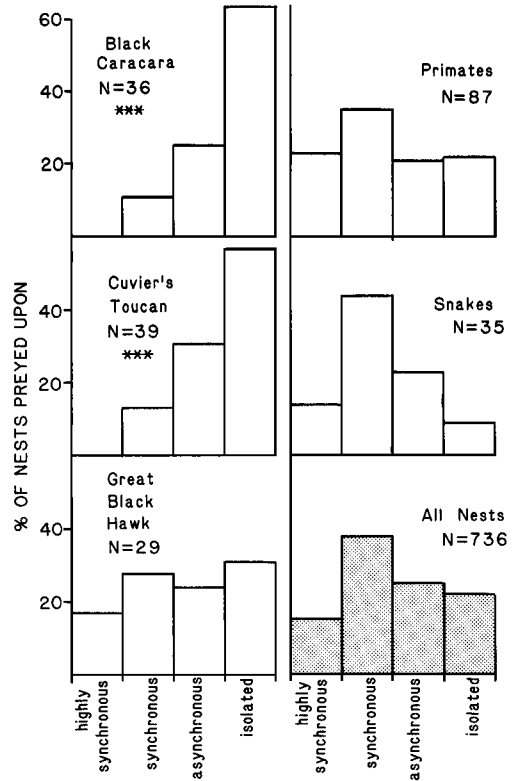

Fig. 5. Predation vs. position and timing of nests within colonies compared with the number of nests in each category (shaded histogram). See text for definitions of each category. N = number of nests preyed on by each predator based on direct observations and attacks inferred from the way nests were opened (see Table 1 for criteria). Data are from Cocha Cashu only. *** = significantly different at the 0.001 level (χ^2 test, df = 3) from the number of nests in each category.

chronous nests in large groups and many nests in smaller groups. "Asynchronous" nests were those in which incubation began within ± 5 days of 0–1 other nests within a 1-m radius in groups of at least 2 other active nests. This category included nests from both large and small clusters that were isolated in time for at least part of the nest cycle. "Isolated" nests are by definition locally asynchronous because there are no nests within a 1-m radius. These categories are useful because they can be arranged in order of increasing local synchrony.

Local synchrony within colonies provided some protection, but only against Black Caracaras and Cuvier's Toucans (Fig. 5). Both of these predators took spatially isolated nests significantly more often than would be expected if they took nests at random with respect to position (Black Caracara: $\chi^2 = 18.2$, df = 1, $P < 0.001$; Cuvier's Toucan: $\chi^2 = 17.0$, df = 1, $P < 0.001$). Caracaras and toucans also took asynchronous nests within clusters significantly more often than synchronous (including highly synchronous) nests within clusters (Black Caracara: $\chi^2 = 8.01$, df = 1, $P < 0.01$; Cuvier's Toucan: $\chi^2 = 9.80$, df = 1, $P < 0.01$). However, neither caracaras nor toucans took asynchronous nests within clusters more often than expected from the overall proportion of synchronous and asynchronous nests in clusters (Fig.

5: Black Caracara: $\chi^2 = 0.02$, df = 1, $P > 0.10$; Cuvier's Toucan: $\chi^2 = 0.26$, df = 1, $P > 0.10$).

Locally synchronous nests probably were less vulnerable to toucans and caracaras because more caciques defended clustered than isolated nests. Great Black-Hawks, primates, and snakes, which caciques do not mob, took nests in proportion to their occurrence in different positions (Fig. 5).

However, I could not separate the effects of nest position and timing from those of colony size with the available data. I have seen caciques chase toucans away from clusters of 4, 7, and 10 active nests, none of which was separated by more than 0.5 m from its nearest neighbor. I never saw a toucan successfully
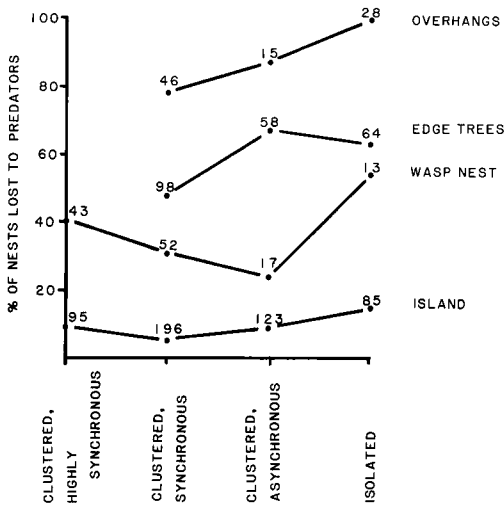
Fig. 6. Percentages of nests taken by predators in different positions and degrees of synchrony within clusters in each of the major colony sites on Cocha Cashu. Numbers above dots are sample sizes. See text for explanation of each category.

open an active nest that was surrounded by more than 2 other active nests within a 1-m radius. I did see a successful attack by a family of caracaras on a cluster of 8 active nests. However, it took over 3 h for the caracaras to open the first nest. During this period caciques supplanted the caracaras from 5 different nests 27 times by pecking them on the undertail coverts and rump. When the caracaras returned the next day, it took only about 90 min to open the next nest. In subsequent attacks on the same group, nests were opened in only about 15 min each. After each nest was opened, the nest owner stopped mobbing. This suggests that as fewer and fewer females mobbed the caracaras, they needed less and less time to open the nests. Thus, the major advantage of clustering nests may be that it maximizes the number of mobbers.

Local synchrony provided no additional protection for nests in large colonies. In island and wasp-nest colonies, which usually were large, there were no significant effects of local synchrony on predation (Fig. 6: Chi-square test, $P > 0.05$ for all comparisons). Within smaller edge-tree colonies, asynchronous nests suffered significantly more predation than clustered, synchronous nests (Fig. 6: $\chi^2 = 4.02$, df =

1, $P < 0.05$), but there were no effects of synchrony within clusters on overhangs (Fig. 6: $\chi^2 = 0.59$, df = 1, $P > 0.10$). Isolated nests in overhanging-branch colonies, however, suffered significantly more predation than clustered synchronous (Fig. 6: $\chi^2 = 6.35$, $P < 0.05$) and asynchronous (Fig. 6: $\chi^2 = 4.26$, $P < 0.05$) nests. These data suggest that local synchrony may be important only in colonies that are small enough to be vulnerable to Black Caracaras and Cuvier's Toucans.

Nesting in clusters may provide protection against Great Black-Hawks for different reasons. The best defense against Great Black-Hawks may be for caciques to nest in densely interwoven clusters that contain a mixture of active and empty nests. When Great Black-Hawks attacked a colony, they searched both active and abandoned nests by shaking them. This behavior may provide information about the presence or absence of large nestlings. In 5 attacks I witnessed, the Great Black-Hawks left the colony after shaking 3–5 nests that were abandoned or contained eggs. One of these colonies contained 12 nests with nestlings, but the hawk did not find them. Great Black-Hawks also appeared to experience difficulty searching clusters of interwoven nests, possibly because they could not shake each nest individually. During one attack on a cluster of 23 interwoven nests, a hawk tore open 2 nests that were empty and then left the tree. Fourteen of the 23 nests in this group contained nestlings, but all were mixed in with empty nests or nests with eggs. At the end of the attack, the hawk tried to attack the cluster of nests from underneath, but it was unable to hang on long enough to tear open a nest. All 4 attacks I witnessed on interwoven groups of more than 6 nests were unsuccessful. The only successful attack by a Great Black-Hawk occurred in a colony in which 28 of 38 nests contained nestlings, and only 5 were interwoven with other nests. The hawk found nestlings in the first 3 nests it opened, after which it returned 7 times over the next 4 days, preyed upon 18 nests, and incidentally knocked another 3 into the water. It gave up after shaking 4 abandoned nests even though there were still 4 active nests with nestlings. Thus, active nests can be hidden from Great Black-Hawks amid abandoned nests. The large number of abandoned nests in old island colonies may effectively hide nests with nest-

lings from Great Black-Hawks. This may explain why these hawks prey on so few of the nests available in island colonies (see Table 2).

None of the defenses against avian predators described above would be effective without enclosed nests. Toucans and caracaras can open most nests, but only after a long period of tearing and pulling during which they are vulnerable to mobbing attacks by caciques. Thick, enclosed nests therefore provide caciques with the time necessary for mobbing to be effective. The difficulty of searching inside enclosed nests also provides caciques with the opportunity to hide their nests from Great Black-Hawks. Clearly, if a hawk could see inside a nest, it would be easy to locate nests with large nestlings. Enclosed nests are also a sufficient defense against many potential hit-and-run predators. I have seen three species of aracari, the Chestnut-eared (*Pteroglossus castanotis*), Curl-crested (*P. beauharnaesii*), and Lettered (*P. inscriptus*), tear at abandoned cacique nests without ever opening one. Three aracari attacks on active colonies I witnessed were speedily repulsed by caciques, which chased them out of the tree. Similarly, enclosed nests provide protection against other potential predators such as Great Egrets (*Casmerodius albus*), which often perch in colony trees and occasionally poke at nests. These attacks are seldom successful because egrets cannot tear holes in nests and cannot reach the young through the nest entrance, which is in the side near the top. The only successful attack by a Great Egret I witnessed occurred in a nest that had its entrance in the top rather than the side. The egret used its long bill to spear the nestling through the entrance hole. This same egret later searched the rest of the nests in that colony, but could not reach any other nestlings.

COLONY SWITCHING BY FEMALES
FOLLOWING NEST LOSS TO
PREDATORS

By switching colonies following nest losses to predators, caciques can protect themselves against their major nest predators. Caciques almost always switched colonies or left the Cocha Cashu area following the loss of a nest to predators (Table 5). Conversely, females that fledged young returned to the colony where they had nested significantly more often than

TABLE 5. Effect of fate of most recent nesting attempt on subsequent nesting attempts within a breeding season.[a]

Fate of previous nest	Renesting attempt in		
	Same colony	New colony	New area[b]
Fledged	48	10	0
Preyed upon	1	70	20

[a] $\chi^2 = 91.6$, df = 1, $P < 0.001$.
[b] Females known to be alive that did not return to nest on Cocha Cashu.

those that did not (Table 5). Following the loss of a nest to a particular predator, caciques tended to shift to a colony site that was well protected against that predator (Table 6). For example, following predation by primates, 23 of 26 caciques switched to island colonies (Table 6) where they were safe from arboreal mammals. Similarly, when attacked by toucans and caracaras, 14 of 20 caciques switched to the large island colony (Table 6), which these predators rarely attacked. Females that switch to island colonies can gain further protection against Great Black-Hawks by hiding their nests amid the numerous abandoned nests left over from earlier in the season. These relatively simple decision rules explain why sites that suffered the least predation, i.e. islands, attracted the largest number of females (see Table 3) and suffered the least predation (see Table 2).

As a result of these decision rules, cacique colony choice "improves" within a season. Caciques started each breeding season scattered among many colony sites (Fig. 7). However, as the season progressed, there were significantly fewer active colonies (Fig. 7) as females abandoned sites that had been attacked by predators and switched to those that had not. By the end of the season, usually only island and wasp-nest colonies were still active.

When predators such as Great Black-Hawks and snakes attack the island colony, females that lose nests tend to leave the area entirely. Of the 24 females that lost nests on the island colony, 14 left the Cocha Cashu area for at least one month (all were known still to be alive), compared with only 4 of 46 that lost nests in other kinds of colonies ($\chi^2 = 20.3$, df = 1, $P < 0.001$). It therefore may be advantageous for females to leave an area when predators such

TABLE 6. Effects of the loss of nests to different predators on subsequent nesting attempts within a breeding season.

Predator	Switch to island	Switch to other colony	Leave area[a]	Return to same colony
Great Black-Hawk	0	4	7[b]	0
Cuvier's Toucan	6	0	1	1
Black Caracara	8	3	2	0
Snake	4	2	7[b]	0
Primate	23	2	1	0

[a] Females that disappeared for at least 1 month but were known to be alive.

[b] All females that lost nests on island colony.

as Great Black-Hawks and snakes, which can attack any site, are active.

DISCUSSION

ADAPTATIONS THAT REDUCE NEST PREDATION

Coloniality in the cacique reduces nest predation in three ways. First, coloniality allows many females to nest in the limited number of sites that are safe from predators. Second, by crowding together in space and time, females enhance the effectiveness of group defense. Third, by nesting in densely interwoven clusters females can hide their nests from some avian predators.

Selection of predator-free habitat.—In areas where nest sites that are inaccessible to mammals are scarce, females may nest together, even if it increases competition for food (Orians 1961, Lack 1968, Snapp 1976). Because of the extraordinary abundance and ubiquity of primates and nocturnal arboreal mammals in the Cocha Cashu area (Terborgh 1983), all birds must find ways to avoid mammalian predators. Caciques can avoid mammalian predators only by nesting in sites that are isolated from the forest or by nesting around wasp nests. The scarcity of such sites intensifies intraspecific competition and may produce local aggregations of nests. Indeed, coloniality in caciques and the closely related oropendolas (*Psarocolius* spp.) may initially have evolved in response to the scarcity of isolated trees and wasp nests. Many species of waterfowl also form dense nesting aggregations on relatively predator-free islands (Duebbert et al. 1983, Hines and Mitchell 1983).
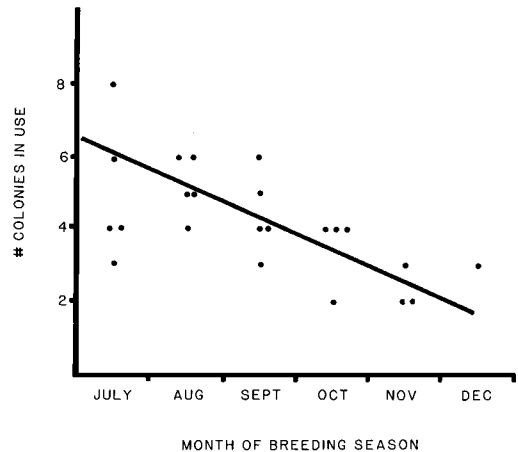

Fig. 7. The number of active colonies in use on Cocha Cashu during July–December (Spearman rank correlation, $r = -0.52$, $P < 0.02$). A colony had to be in use for at least 5 days to be considered active during a particular month. I include only months in which I was present for the entire period.

Increased effectiveness of group defense.—The scarcity of sites that are safe from mammals does not explain why caciques clump their nests within the space available for nesting. In the Yellow-rumped Cacique, clumping nests in space and time increases the effectiveness of mobbing. It may be significant that oropendolas often do not clump their nests within colonies (Koepcke 1972, Robinson pers. obs.). Lone oropendolas are capable of chasing away Black Caracaras and Cuvier's Toucans (Robinson pers. obs.), which means that they do not need to clump their nests together to deter these predators. Lemmetyinen (1971), Hoogland and Sherman (1976), Veen (1977), and Gross and MacMillan (1981) also hypothesized that tight clumping of nests may increase the effectiveness of mobbing. This study is the first, however, in which large groups of birds were observed to be more successful at chasing away predators than small groups. Dominey (1981) showed that bluegill sunfish (*Lepomis macrochirus*) were more successful at chasing away predators from large colonies than they were from small colonies.

Position effects.—Because of the irregular shape of clusters of cacique nests, I cannot test directly for "selfish-herd" effects, i.e. differences in predation rates between central and peripheral nests. Selfish-herd effects can work only against nonrecruitable predators that can be sa-

tiated by a relatively small proportion of the nests available at any one time (Hamilton 1971). Most predators of the cacique, however, are highly recruitable, and many can destroy an entire colony in a short period. If predators find young in a peripheral nest, they are very likely to return to that group until they have searched all or nearly all the nests. Nests in large, highly synchronous clusters, which presumably have more "central" nests, fare no better than those in smaller, less synchronous groups (see Fig. 6). Selfish-herd effects therefore may be a relatively unimportant advantage of coloniality in the cacique.

Position effects, however, can be important in other ways. Because cacique nests are enclosed and often stay on a tree for months after they have been abandoned, caciques can effectively hide active nests among empty nests. This defense works very well against the Great Black-Hawk, which checks relatively few nests before giving up and leaving a colony. Indeed, the Troupial (*Icterus icterus*), a nest pirate, not only takes over an active cacique nest for its own use, but also takes over all the nests surrounding it, in effect creating a maze of empty nests that hide its eggs and young (Robinson 1985; see also Pearson 1974). Toward the end of the breeding season, many caciques build their nests in groups of abandoned nests. Predators also may be much less likely to attack a cluster consisting mostly of old, abandoned nests.

Predator satiation.—When nesting is highly synchronous and colonies are large, some non-recruitable predators can be satiated before taking all of the available nests. The best evidence that extreme synchrony can satiate predators comes from studies that show reduced proportions of nest predation during the peak of the breeding season (Patterson 1965, Robertson 1972, Nisbet 1975, Veen 1977, Nisbet and Welton 1984). In the Yellow-rumped Cacique, nesting is spread fairly evenly throughout the nesting season (see Fig. 2) and therefore is not highly synchronous. From mid-July through early February there are usually only 40–100 active nests in the Cocha Cashu area. Most predators of the cacique would be capable of preying on all of the active nests if they could reach them or if caciques did not defend their nests. Indeed, highly synchronous nests within colonies suffer about the same level of predation as synchronous nests (see Fig. 6). From this

I conclude that predator satiation is very unlikely to be an important advantage of coloniality in the Yellow-rumped Cacique.

COLONY SWITCHING AND HABITAT STABILITY

The flexibility of colony site selection in caciques suggests that they are well adapted to nesting in "unstable" habitats (*sensu* McNicholl 1975). The distribution of cacique nests at any one time reflects the availability of ephemeral sites such as wasp nests and the recent predation history of the area. Colony switching in the cacique almost always involves individuals moving to safer colony sites within breeding seasons. Most caciques that lose nests to a predator switch to island colonies that are safe from most predators. On those infrequent occasions when predators successfully attack the island colony, most females leave the Cocha Cashu area rather than switch to more vulnerable sites. When the safest sites in an area are no longer safe, it may be better for females to leave in search of another area where predators have been less active. Several other studies have shown that birds switch to new nest sites following predation (Harvey et al. 1979, Burger 1982, Greig-Smith 1982). This is the first study, however, to show that birds usually switch to nest sites that are safer from the predator that took their nest.

It is not clear from these considerations why caciques ever nest in sites other than predator-free islands and wasp nests. Intrasexual aggression provides the proximate explanation for the presence of females in poor nesting habitats. Many females are aggressively excluded from the best nest sites by larger females (Robinson in press). Most of these females are forced to nest in more vulnerable colony sites or in more vulnerable sites within colonies. Intrasexual aggression therefore forces females to spread out among several colony sites, while nest predators promote clumping. The ultimate adaptive value of the exclusion of females from colonies is less clear. Beyond a certain point, increased group or colony size provides no further defenses against predation (Figs. 3, 6). Once there are enough females to chase away caracaras and toucans, any more nests would increase food competition near the colony with no added benefits. Food competition therefore may place an upper limit on the number of

females that can nest in a given colony at any one time. Competition should be especially severe early in the breeding season, when fruit and insects are relatively scarce (Terborgh 1983). Thus, the tendency for caciques to scatter nests among many colony sites early in the season (Fig. 7) may result from the reduced carrying capacity of the areas around the best colony sites.

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