

FORAGING ECOLOGY AND HOST RELATIONSHIPS OF GIANT COWBIRDS IN SOUTHEASTERN PERU

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ABSTRACT.—I studied the foraging ecology and host relations of a population of brood parasitic Giant Cowbirds (*Scaphidura oryzivora*) in the undisturbed Manu National Park of Amazonian Peru. Giant Cowbirds foraged mostly along rivers and lakes where they searched for arthropods, fruit, and nectar. Male cowbirds sometimes foraged on the backs of mammals on which they captured biting flies. The two potential host species, the Russet-backed Oropendola (*Psarocolius angustifrons*) and Yellow-rumped Cacique (*Cacicus cela*) defended their colonies against cowbird parasitism, regardless of colony location. Giant Cowbirds concentrated most of their visits on oropendola nests, which were sometimes left untended when the colony members were foraging together in a flock away from the colony. Yellow-rumped Caciques, however, seldom left their colonies untended and no cowbirds were known to fledge from cacique nests during the five years of the study. This situation differs markedly from that reported by Smith (1968, 1979, 1980) in Panama where Giant Cowbirds parasitized both oropendolas and caciques, and at least some hosts did not chase cowbirds away from their nests. I argue that the major difference between the two study areas is that in Peru, both caciques and oropendolas generally raise only a single young, which means that there can be no advantage to being parasitized as there is in Panama. Received 29 July 1987, accepted 18 Dec. 1987.

One of the most remarkable examples of coevolution ever described is the relationship between the brood parasitic Giant Cowbird (*Scaphidura oryzivora*) and its colonial hosts, the Yellow-rumped Cacique (*Cacicus cela vitellinus*) and various oropendolas (*Psarocolius* spp.) in Panama (Smith 1968, 1979, 1980). Smith found that some Giant Cowbirds were not aggressively chased away from nests in colonies that were unprotected by wasp nests. These cowbirds laid nonmimetic eggs, and the nestling cowbirds cleaned botfly (*Philornis* spp.) larvae, which burrow into nestlings, from their nest mates (Smith 1968). As a result, parasitized nests fledged more host young on average than unparasitized nests. Cowbirds, however, were aggressively chased away from colonies protected by wasp nests, perhaps because the wasps provide protection against botflies. Only stealthy cowbirds that laid mimetic eggs could gain access to and parasitize nests in colonies protected by wasps. Smith concluded that it is to the hosts' benefit to allow their nests to be parasitized, but only in nests unprotected by wasps. In response to this situation, the Giant Cowbird has evolved behavioral and egg-color polymorphisms.

In this paper, I describe the foraging ecology and host relationships of

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the Giant Cowbird in an undisturbed section of Amazonian Peru. At this site, Giant Cowbirds regularly visited colonies of two potential host species, the Yellow-rumped Cacique (*C. c. cela*), and the Russet-backed Oropendola (*Psarocolius angustifrons*), but were known to parasitize only the oropendola.

STUDY AREA AND METHODS

This study was conducted in the Manu National Park in the Department of Madre de Dios, southeastern Peru at 11°51'S, 71°19'W. All observations were made in the vicinity of the Cocha Cashu Biological Station, an area of undisturbed lowland floodplain forest of the Manu River. The study area includes an oxbow lake (Cocha Cashu) and a section of the Manu River (see Fig. 1). Terborgh (1983) described the vegetation and climate of the Cocha Cashu area.

This study was conducted during 24 months in the field, 1979–1984, as part of a study of the social behavior of the Yellow-rumped Cacique and other colonial Icterinae (Robinson 1984, 1985a, 1986a). I visited each active colony daily and recorded the phenology, fates, and positions of each nest (see Robinson 1985b). Caciques, oropendolas, and cowbirds were captured in mist nets placed near active colonies and roost sites. During the study I caught 8 cowbirds, 10 oropendolas, and over 700 caciques. All captured individuals were color-marked. Whenever cowbirds were observed at host colonies, I recorded the following data: date, number of cowbirds, host reaction, and any behavior patterns used by cowbirds to gain entrance to host nests. Contents of all oropendola nests and most cacique nests were not checked because they were too high, though I have checked nest contents of 106 low cacique nests. For this reason, I have no data on eggs, egg mimicry, or percentage of oropendola nests parasitized.

In 1982, as part of a larger census of the Cocha Cashu bird community (see Terborgh 1985), the locations and activities of any Giant Cowbirds observed were recorded in the 115-ha area shown in Fig. 1. The census area is crisscrossed by trails located 100–200 m apart, each of which was covered at least 20 times during the mid-August to mid-November census period. Once a week in 1982, I also paddled my boat around the entire lake and recorded the locations of Giant Cowbirds. Whenever I observed a cowbird foraging, I recorded its location, sex, height, and the substrate on which it was searching for prey. I used only the first observation from each independent sequence for statistical analyses.

HOST SPECIES

Russet-backed Oropendolas usually nested together with Yellow-rumped Caciques in the same or adjacent trees (Robinson 1985a). The two potential host species generally coexisted peacefully and often built their pendent, pouchlike nests close together, though in some years male oropendolas defended sections of colony trees against caciques (Robinson 1985a). Colonies were situated in isolated trees in the lake bed and in the forest (Fig. 1). Most colony sites provided protection against arboreal mammals such as monkeys, which often attacked colonies in less isolated positions (Robinson 1985b). Within colonies, caciques clustered their nests together and mobbed avian nest predators such as Cuvier's Toucan (*Ramphastos cuvieri*) and the Black Caracara (*Daptrius ater*) (Robinson

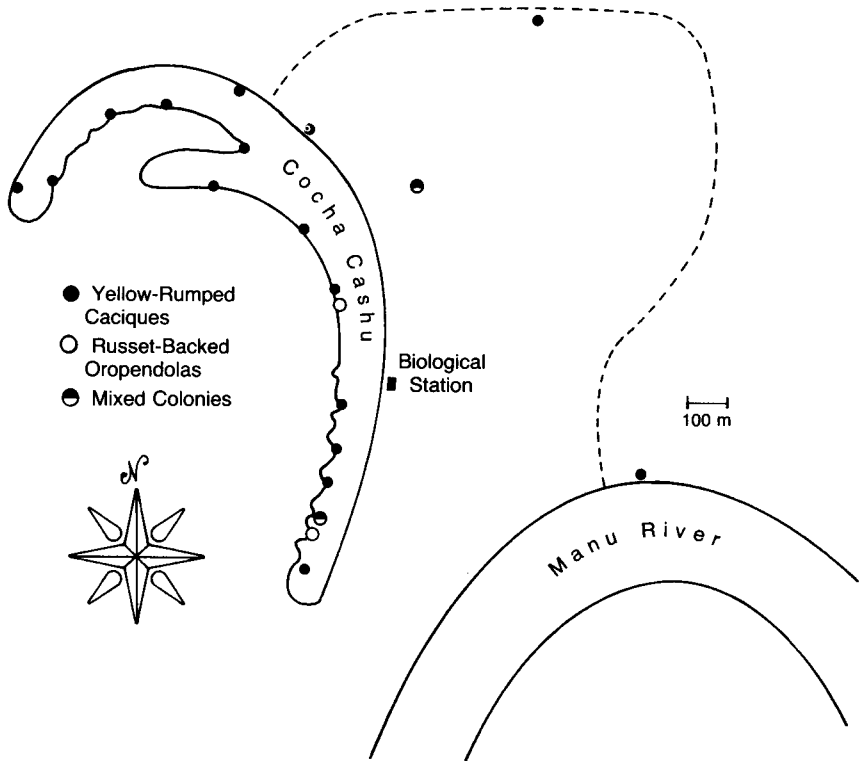


FIG. 1. Map of study area showing locations of colonies of Yellow-rumped Caciques (closed circles), russet-backed Oropendolas (open circles), and mixed colonies (half open circles). Dashed line encloses area censused in 1982.

1985a). Oropendolas, however, often scattered their nests throughout a colony tree, perhaps because lone oropendolas, which are 2–6 times heavier than caciques (Robinson 1985a), are large enough to chase away most avian predators (Robinson 1986a). None of the colonies studied in 1981 and 1982 was located around wasp nests.

Cacique nests were generally continuously available to cowbird parasitism during the breeding season, while most oropendola nests were available for only brief periods (Fig. 2). Oropendola nesting was significantly more synchronous than that of the cacique (Fig. 2; Kolmogorov-Smirnov test, $\chi^2 = 16.4$, $P < 0.001$). The majority of oropendolas began nest-building within three of the 15-day periods (Fig. 2). In 1981, I estimated that 114 different female caciques nested on Cocha Cashu, compared with only 28 female oropendolas.

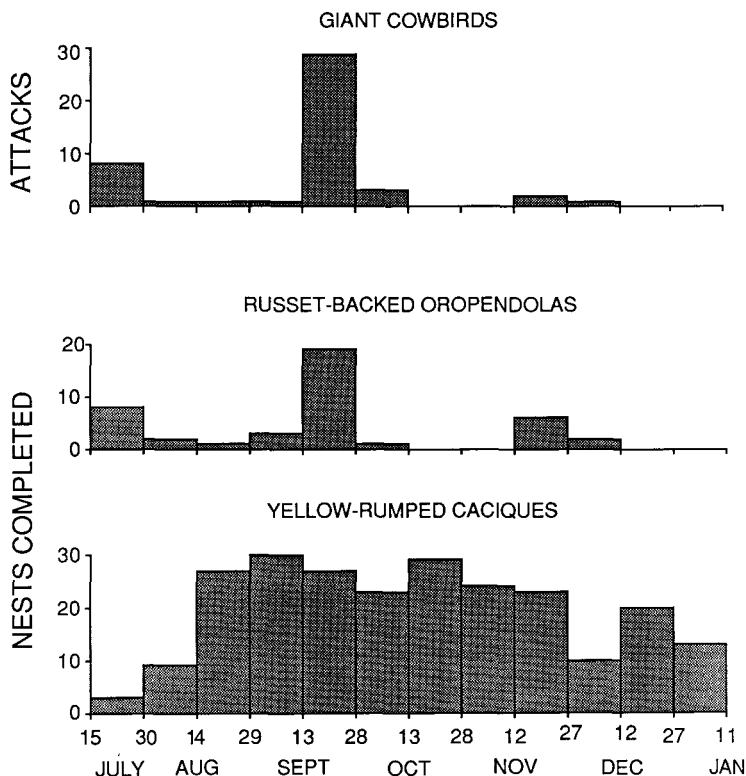


FIG. 2. Phenology of nests (number completed per 15-day period) of Yellow-rumped Caciques and Russet-backed Oropendolas compared with frequency of attacks by Giant Cowbirds (number observed during 2-h samples each day), 1981. All colonies under observation were at the south end of Cocha Cashu.

Casqued (*P. oseryi*), Crested (*P. decumanus*), and Olive (*P. yuracares*) oropendolas also occurred in the Cocha Cashu area. J. Leak (pers. comm.) observed no cowbird visits at two forest colonies of Casqued Oropendolas. However, I have no data on the relationships between Giant Cowbirds and the other two species of *Psarocolius*.

RESULTS

Foraging ecology.—Giant Cowbirds foraged in small flocks (Table 1) near water and generally avoided the forest interior (Fig. 3). Cowbirds were generalized in their diet, substrate use, and tactics used to catch prey. Cowbirds ate fruit (chiefly two moraceous species, *Ficus trigona* and *Coussapoa*), nectar (chiefly *Combretum* and *Quararibea*), and arthropods.

TABLE 1
FLOCK SIZES OF GIANT COWBIRDS WHEN FORAGING AND
ATTACKING HOST COLONIES

Flock size	Percentage	
	Foraging	Visiting colonies
1	28.9	61.4
2-4	18.4	34.1
5-8	23.7	4.5
9-12	21.1	0.0
>12	7.9	0.0
	N = 88	N = 38

Cowbirds used three very different foraging tactics when searching for arthropods: (1) Terrestrial foraging. Cowbirds often walked along the shore of Cocha Cashu and along river beaches exposed during the dry season. When foraging along the lake shore, cowbirds both gleaned small prey from the surface and turned over leaves with their beaks. When foraging on beaches, cowbirds walked along the sand and gleaned small insects and probed in piles of driftwood. I have seen as many as 80 Giant Cowbirds foraging together along the beaches of the nearby Alto Madre de Dios River. The largest flock I ever observed on the Manu River consisted of 26 individuals. (2) Foliage searching. When foraging along the lake margin, cowbirds often searched branches and foliage up to 10 m above the water. Males generally searched branches more than females (Table 2, $\chi^2 = 10.84$, $df = 2$, $P < 0.001$), where they used their beaks to tear off strips of bark. Females searched significantly more living and dead leaves (Table 2) where they used their beaks to probe into curled leaves and extract hidden prey. (3) Foraging on mammals. Giant Cowbirds regularly foraged for insects on the backs of capybaras (*Hydrochoerus hydrochoerus*), a large aquatic rodent that occurs primarily in marshes along the edge of the lake (Fig. 3). Capybaras allowed cowbirds to feed on their backs, presumably because cowbirds eat the biting horse flies (Tabanidae) that swarm around capybaras during the day. In one 12-min observation period, a male cowbird caught 24 large (1.5–2.5 cm) tabanids. During part of this period, the capybara elevated its head at a 45° angle, closed its eyes, and allowed the cowbird to walk on its nose. Capybaras would not, however, allow cowbirds to probe in their fur; each time this happened, the capybara rolled over on its side, or shook itself. I also once saw a Giant Cowbird foraging on the back of a tapir (*Tapirus terrestris*).

TABLE 2
SUBSTRATES SEARCHED BY MALE AND FEMALE GIANT
COWBIRDS WHEN FORAGING IN FOLIAGE

Substrate	Percentage	
	Males	Females
Living leaves	4.8	25.8
Dead leaves	45.2	54.8
Dead branches	50.0	19.4
	N = 42	N = 31

Raids on host colonies.—Cowbirds usually visited colonies either singly or in small groups (Table 1). Before visits, the foraging flocks split up, some individuals staying behind and others moving towards colonies (Table 1; foraging flocks are significantly larger than flocks that visit colonies, $P < 0.001$, $\chi^2 = 40.2$).

Female Giant Cowbirds most often visited the nests of Russet-backed Oropendolas. Of 88 separate visits to active colonies witnessed, only two were directed at nests of the Yellow-rumped Cacique; all others were directed at oropendola nests. Similarly, cowbirds concentrated most of their visits on colonies when oropendolas were completing nests (Fig. 2). The frequency of cowbird visits differed significantly from the frequency of caciques completing nests during each period (Kolmogorov-Smirnov Test, $\chi^2 = 39.9$, $P < 0.001$). The distribution of cowbird visits did not, however, differ significantly from the frequency of oropendola nests completed during each period (Kolmogorov-Smirnov Test, $\chi^2 = 2.42$, $P > 0.20$).

Both caciques and oropendolas aggressively chased cowbirds out of colonies. Of 88 visits witnessed, cowbirds were chased away 74 times by oropendolas of both sexes and by male caciques. On 9 occasions, male caciques chased cowbirds away from undefended oropendola nests, which suggests that oropendolas may derive an antiparasitic benefit from nesting with caciques. On 8 of the remaining 14 visits, cowbirds left the colony before they either entered a nest or were chased away. Only 6 of the 88 visits resulted in a female cowbird's entering an oropendola nest. All six visits occurred when the oropendolas were away foraging. One of these nests later fledged a cowbird. The most successful cowbird visit occurred when a flock of three females and a male flew into an undefended colony, and the females entered three nests in which incubation had just begun. There were no caciques nesting in this colony tree.

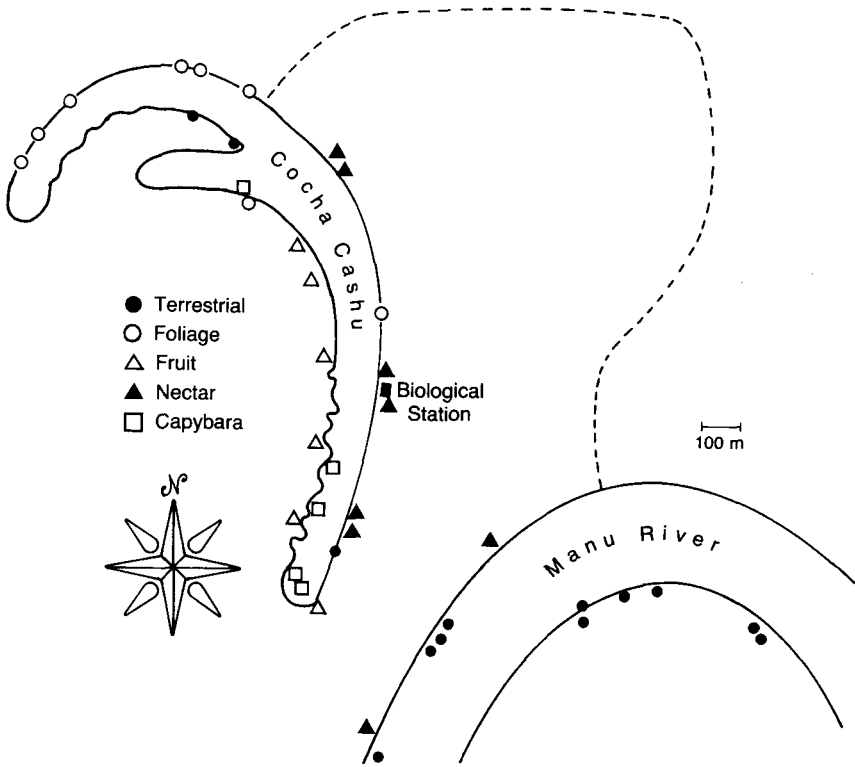


FIG. 3. Locations of foraging observations of Giant Cowbirds, 15 August to 12 November, 1982.

When cowbirds visited colonies as a group, males sometimes seemed to lure oropendolas away from their nests, while females then entered the untended nests. On one visit, a male cowbird flew up to a group of oropendola nests where a male and female oropendola were sitting. The cowbird perched nearly vertically within less than 0.5 m from the male oropendola, and it puffed up its head and neck feathers, a display similar to that used during courtship (described in Skutch 1954). Both the male and female oropendola then started chasing the cowbird out of the tree. As soon as the chase began, two female cowbirds flew up to the untended nests and looked inside. The female oropendola returned before the cowbirds entered any of the nests. On five other occasions, I saw females approach nests when the oropendolas were chasing male cowbirds. N. Smith (pers. comm.) has observed similar behavior in Panama.

Three other group visits involved what appeared to be coordinated

efforts among female cowbirds. In each of these visits, one of the females entered a nest containing an incubating female, which resulted in a chase. The other female cowbirds then flew up to the nest as soon as the female oropendola was out of the nest. Each time the second female cowbird was about to enter the nest, she was chased away by male caciques. Chapman (1928) and Skutch (1954) also described group visits by cowbirds.

On two occasions, cowbirds entered oropendola colonies during attacks by a juvenile Bicolored Hawk (*Accipiter bicolor*), which frequently chased oropendolas. Both times, however, the oropendolas returned before the cowbirds entered any nests.

Cowbirds appeared to have considerable difficulty entering cacique nests. I twice saw female cowbirds in recently abandoned cacique colonies. These females poked their heads into six nests but only succeeded in entering one. One female cowbird appeared to become trapped halfway into a nest before giving up and leaving. The entrances in cacique nests may be too small for most cowbirds in Peru.

Giant Cowbirds appeared to have a minimal impact on their hosts in the Cocha Cashu area during this study. None of the 168 female caciques I observed with fledglings was feeding cowbirds, and only 3 of 24 oropendola families were feeding a cowbird. All 24 oropendola females fed only a single fledgling, whether it was a cowbird or an oropendola. Similarly, none of the 106 cacique nests I have checked during incubation contained a cowbird egg.

DISCUSSION

Host relationships in Panama and Peru.—The host relationships described in this paper differ considerably from the situation described by Smith (1968, 1979, 1980) in Panama. In Peru, Giant Cowbirds specialized on oropendolas and seemed to avoid the far more abundant Yellow-rumped Cacique. In contrast, cowbirds regularly parasitized both caciques and oropendolas in Panama and elsewhere in Central America (Skutch 1954, Smith 1968). In southeastern Peru, both caciques and oropendolas chased away cowbirds, regardless of whether or not their colonies were protected by wasps. Cowbirds used a variety of tactics to enter host nests, all of which involved stealth or possibly distraction. I never saw caciques or oropendolas passively allow a Giant Cowbird to enter a nest, even though many cacique nestlings have heavy botfly infestations, and none of the colonies I studied was protected by wasps or bees (Robinson, unpubl. data). In Panama, on the other hand, oropendolas show little aggression towards cowbirds in colonies that are unprotected by wasps. It is, however, difficult to separate the effects of cowbirds on caciques and oropendolas because Smith (1968) lumped the two host species together.

Why, then, do cowbirds specialize on oropendolas in Peru? The answer to this question may be related to the different social organization of the two potential host species. In Peru, most female oropendolas from a colony foraged together in a flock (Robinson 1986a, unpubl. data); males often accompanied these flocks (Robinson 1986a). As a result, oropendola colonies were often vacant when the flock was away foraging. During such times, oropendola nests were open to attacks by cowbirds. Cacique females, on the other hand, foraged singly or in small flocks, and generally did not leave the colony in a single flock (Robinson, unpubl. data). Dominant males consorted and defended each female separately, and low-ranking males spent much of the day singing and displaying in colonies (Robinson 1986c). As a result, large (>20 nests) cacique colonies were seldom vacant and were, therefore, protected most of the time. Oropendolas appeared to derive a considerable benefit from nesting with caciques. In this context, it is curious that oropendolas often nested apart from caciques and occasionally defended sections of colony trees against caciques (Robinson 1985a).

Why do caciques and oropendolas chase away cowbirds? Perhaps the major reason why there are no "dumper" cowbirds in the Cocha Cashu area is that both caciques and oropendolas generally only fledge a single young (Robinson 1986b, unpubl. data). In order to raise nestlings, cacique females greatly accelerated their foraging rate, lost weight, and even then generally only raised one young from a clutch of two (Robinson 1986b). These data suggest that females can only obtain sufficient food to raise a single young. Under such circumstances, there can be no benefit in raising a cowbird nestling even though botflies may pose a serious problem. It is unlikely that a cacique could raise both a cowbird and its own young, especially because cowbirds are larger than caciques (Robinson, unpubl. data). It is much more likely that a female oropendola could raise both a cowbird and an oropendola, especially because cowbirds are smaller, but I never saw a female oropendola with a mixed family. In contrast, both caciques and oropendolas routinely raised more than one young in Panama, and mixed families occurred commonly (Smith 1968). Smith artificially augmented clutches in Panama and found that caciques and oropendolas could raise more than two young. For unknown reasons, caciques and oropendolas may be less food limited in Panama than in Peru. It is also possible that the three other species of oropendolas in Amazonian Peru (*P. yuracares*, *P. oseryi*, and *P. decumanus*) have different relationships with the Giant Cowbird than the Russet-backed Oropendola.

Foraging ecology and brood parasitism.—Brood parasitism in birds is often associated with unusual diets and foraging tactics (reviewed in Hamilton and Orians 1965, Payne 1977, May and Robinson 1985). Brown-

headed Cowbirds (*Molothrus ater*), for example, historically followed herds of nomadic ungulates, a behavior that may have predisposed them towards the evolution of brood parasitism (Mayfield 1965). By parasitizing the nests of other species, Brown-headed Cowbirds could reproduce without staying for long in one place. Alternatively, the evolution of brood parasitism may have made such a nomadic niche possible. Giant Cowbirds also foraged with mammals, and most of their foraging is concentrated in a narrow belt along rivers and lakes in microhabitats that vary in availability with fluctuations in water levels. Within the available microhabitats, cowbirds wander widely, sometimes foraging one or more km from the colonies that they visit. The brood parasitic habits of the Giant Cowbird may make it possible both to reproduce and exploit temporally variable resources that are scattered along the narrow edges of rivers and lakes.

The evolution of host specialization in Giant Cowbirds.—Hamilton and Orians (1965) hypothesized that three conditions would favor the evolution of brood parasitism: (1) the potential parasite is closely related to the host, which increases the chances that the nestling diet will be appropriate, (2) the parasite is rare relative to the host, and (3) the host is a colonial nester because these species show reduced territorial behavior and their nests are easy to find. The Giant Cowbird association with both oropendolas and caciques clearly fits all of these criteria. Cowbirds are in the same subfamily as oropendolas, and both eat essentially the same kinds of food (Robinson 1985a, unpubl. data). Giant Cowbirds are considerably less common than their hosts and are restricted to bottomland areas along lakes and rivers. At least in Peru, neither oropendolas nor caciques appear to suffer high levels of cowbird parasites. Oropendola and cacique colonies are also very conspicuous and are located close to cowbird feeding areas, though oropendolas defend colonies against cowbirds. In addition, caciques and oropendolas place their nests in sites that are inaccessible to mammals and actively defend their colonies against most avian predators (Robinson 1985b). As a result, a high percentage of their nests escape predation and eventually fledge young. Over 40% of all cacique nests and 50% of all oropendola nests on Cocha Cashu fledged young (Robinson 1985b, unpubl. data), a very high percentage for a tropical bird (cf Oniki 1979, Skutch 1985). Oropendolas and caciques are, therefore, ideal hosts once their antiparasite defenses have been circumvented.

Colonies of caciques and oropendolas also support several other species of birds. Troupials (*Icterus icterus*) and Piratic Flycatchers (*Legatus leucophaius*) pirate oropendola and cacique nests and use them for their own eggs and young (Robinson 1985a). These two species parasitize the nest

building and predator defenses of caciques and oropendolas. Giant Cowbirds go one step further and parasitize both the nests and the parental care of their hosts. In Panama, Giant Cowbirds had further evolved a mutualistic relationship in which some cowbirds actually benefit their hosts by parasitizing them, while others lay host-specific mimetic eggs (Smith 1968). Oropendolas and caciques may also enjoy mutual advantages by nesting together, since both species mob predators, chase away cowbirds, and give loud alarm calls (Robinson 1985a, b, unpubl. data). These parasitic and mutualistic relationships are among the most complex ever described for birds.

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