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INTERSPECIFIC BROOD PARASITISM OF MONTEZUMA OROPENDOLAS BY GIANT COWBIRDS: PARASITISM OR MUTUALISM?[1]

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Obligate interspecific brood parasitism has evolved independently in several avian families (Hamilton and Orians 1965, Payne 1977). Such parasitism generally has a marked negative effect on host fitness (e.g., Post and Wiley 1976, Davies and Brooke 1988, Power et al. 1989, Scott et al. 1992), and the brood parasite and host are usually viewed as being engaged in a coevolutionary "arms race" (Davies and Brooke 1988, Rothstein 1990, Braa et al. 1992). However, Smith (1968, 1979) described a remarkable and complex interdependence between the parasitic Giant Cowbird (*Scaphidura oryzivora*) and two of its hosts in Panama, the Chestnut-headed Oropendola (*Psarocolius wagleri*) and Yellow-rumped Cacique (*Cacicus cela*). In this system, the hosts could apparently benefit from cowbird "parasitism" in some situations.

Smith found that ectoparasitic botflies (*Philornis* spp.) were a major source of mortality for oropendola and cacique nestlings. Cowbird nestlings removed botfly larvae from their nestmates, such that nests with cowbirds fledged more host young than nests without cowbirds. Indeed, in colonies without any other defense against botfly parasitism (i.e., colonies without hymenoptera nests), oropendolas and caciques allowed cowbirds to enter their nests and did not remove the eggs of cowbirds that were discovered (Smith 1968, 1979). This result contrasts sharply with studies of many other brood parasite-host relationships, where hosts actively defend their nests against brood parasites (e.g., Davies and Brooke 1988, Rothstein 1990), and parasites have evolved many behavioral and developmental tactics to circumvent the defenses of their hosts (e.g., Davies and Brooke 1988, Briskie and Sealy 1990, Braa et al. 1992, Scott et al. 1992).

To determine the factors that allow the interdependence described by Smith (1968, 1979) to arise, it is first necessary to determine the distribution of the phenomenon. Giant Cowbirds parasitize several species of oropendolas and caciques (Orians 1985), many of which have a nesting biology similar to that of the hosts studied by Smith (see Chapman 1929, Skutch 1954, Schäfer 1957, Tashian 1957, Drury 1962, Fraga 1989, Webster 1994). If several of these host populations benefit from and allow cowbirds to lay eggs in their nest, then ecological factors common among them must favor the evolution of this interdependence. Alternatively, giant cowbirds may be parasites to most hosts, such that some feature of the populations Smith studied makes the complex mutualism unique to Panama. These possibilities can be distinguished by determining whether other hosts allow Giant Cowbirds to enter their colonies, or whether they actively defend themselves against cowbird parasitism. Only one published study has directly attempted to answer this question (Robinson 1988).

In this note, I examine the possibility that a similar mutualism exists between Giant Cowbirds and one of their primary hosts in Costa Rica, the Montezuma Oropendola (*Psarocolius montezuma*). To do so, I determined whether Montezuma Oropendolas actively defend themselves against Giant Cowbirds and, if so, whether cowbirds show behaviors that might circumvent this defense. Because it was difficult to examine

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the contents of oropendola nests regularly, the effect of cowbirds on the host's reproductive success was not measured.

STUDY SPECIES AND METHODS

Montezuma Oropendolas are large (adult male mass >500 g) passerines that inhabit lowland rainforests through Central America. Like other oropendolas and some caciques, Montezuma Oropendolas nest colonially, with up to 100 or more females building their long, pensile nests in a single tree (Skutch 1954, Fraga 1989, Webster 1991). The nesting colonies of Montezuma and Chestnut-headed Oropendolas are similar in appearance, and they sometimes nest together in adjacent colony trees (pers. obs.). In addition to nesting in a single colony tree, female Montezuma Oropendolas cluster their nests within the colony tree as well: often a dozen or more nests are massed together on single limb (Fraga 1989, Webster 1994). Unlike some oropendolas and caciques, Montezuma Oropendolas do not nest in association with social hymenoptera (Fraga 1989), and none of the nests I observed during this study were built near hymenoptera nests. Chestnut-headed Oropendolas and Yellow-rumped Caciques do nest with hymenoptera, and this behavior apparently protects the birds from botfly parasitism (Smith 1983) as well as from nest predators (Robinson 1985).

I studied a population of Montezuma Oropendolas at the Estación Biológia La Selva, Costa Rica, during each breeding season (January through May) from 1986 to 1990, and collected data on cowbirds starting in 1987. Oropendolas were observed at a focal nesting colony during each season. Whenever a Giant Cowbird entered the vicinity of the observation colony, I and my assistants observed it until it left the colony area. We recorded the time of the visit, the nests that the cowbird visited, any nests that it entered, and the reactions of any oropendolas in the colony. Cases in which two or more cowbirds visited the colony simultaneously were counted as a single visit.

The nesting activities of individual female oropendolas at the focal colony were closely monitored during 1987, 1988 and 1989. However, the focal nesting colony was abandoned early in the 1989 breeding season (Webster 1994), leading to a reduced sample size in that year. In 1987 and 1988, we counted the number of females perched in the colony during scan samples conducted every 20 minutes. Although this figure underestimates the total number of females present in the colony (because females inside of nests could not be seen or counted), it is likely to be correlated with the number of females present and gives a rough measure of the number of females able to defend against cowbirds.

RESULTS

We recorded a total of 88 visits by Giant Cowbirds to oropendola colonies. Although most visits were by single cowbird females, pairs or small groups (up to four individuals) sometimes visited colonies together (17.7% of all cowbird visits). Most cowbird visits were during periods when female oropendolas were lining their nests with leaves (Fig. 1). Nest-lining is the final stage of nest construction, and females presumably lay their eggs during this period (Webster 1994). In 1987, the cowbird visitation rate (number of cowbird visits per hour of observation) during each 10 day period was significantly correlated with the number of females lining nests during that period (Fig. 1, $r = 0.96$, df = 8, $P < 0.01$). This correlation was marginally significant in 1988 (Fig. 1, $r = 0.65$, df = 7, $P = 0.06$), and elimination of a single outlier (days 61–70) makes it statistically significant ($r = 0.86$, df = 6, $P < 0.01$). The correlation between cowbird visits and number of females lining nests was not statistically significant in 1989 (Fig. 1, $r = 0.76$, df = 2, $P > 0.10$), although the abbreviated nesting period in that year was too short for solid conclusions to be drawn.

Cowbirds were not tolerated near nests at any colony. Cowbirds that approached nests were attacked and driven from the colony, and we never saw a cowbird successfully approach or enter a nest when an oropendola was perched in the colony tree. Cowbirds were chased from the colony more often by female oropendolas than by males (75 vs. 26 chases, respectively). This last result may reflect a biased adult sex ratio at nesting colonies rather than a tendency for females to be more aggressive toward cowbirds, as the mean number of males present in the colony during scans (0.87, all years combined) was somewhat lower than the mean number of females visible outside of their nests (1.27) and several other females were often present in the colony but hidden inside of their nests. Cowbirds were able to enter nests during only seven of 83 visits to colonies (only visits in which we could determine success of the cowbird were counted; total of 17 nests entered).

Giant Cowbirds were sometimes tolerated in a colony tree if they did not approach any nests ($n = 7$ cases). Furthermore, a female usually did not chase a cowbird until it approached her own nest: of 35 occasions in which an identified female chased a cowbird, 28 (80%) were chases by a female who had a nest in the cluster where the cowbird was located when the chase began, and only 7 (20%) were by a female with a nest in a different part of the colony. Although not rigorously quantified, females inside of nests usually did not come out of their nest to chase a cowbird until it was very near, possibly because females were unaware of the cowbird's presence or because the cowbird was not a threat.

Relatively few female oropendolas were present in the nesting colony during the late morning and early afternoon hours (Fig. 2), when temperatures at the relatively exposed colony sites were high. The daily pattern of cowbird visitation was significantly different from random (data from all years combined, $\chi^2 = 35.83$, df = 4, $P < 0.001$) and showed the opposite pattern: few visits occurred in the early morning and late afternoon, and most visits occurred during the late morning hours when few females were present to defend their nests (Fig. 2). Although sample sizes were small, this pattern was also statistically significant in 1987 ($n = 25$ cowbird visits, $\chi^2 = 13.91$, df = 4, $P < 0.01$) and 1989 ($n = 32$ cowbird visits, $\chi^2 = 16.46$, df = 4, $P < 0.01$), and of border-line significance in 1988 ($n = 21$ cowbird visits, $\chi^2 = 8.06$, df = 4, $0.05 < P < 0.10$).

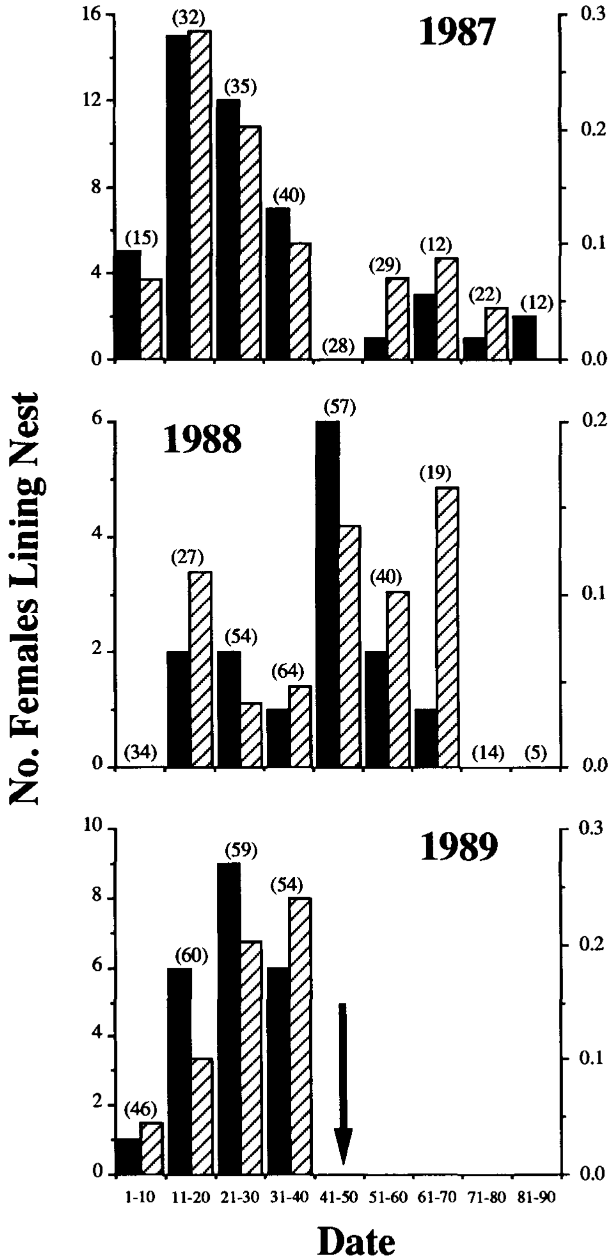

FIGURE 1. Number of females lining nests with leaves (solid bars) and number of cowbird visits per hour of observation (hatched bars) versus date (shown in 10 day blocks) in 1987 (26 active nests, day 1 = Jan. 30), 1988 (12 active nests, day 1 = Jan. 12) and 1989 (22 active nests, day 1 = Jan. 15). In each year, day 1 is the first day of observations and approximately equals the initiation of nest building in that season. Numbers in parentheses are the total number of hours of observation during each time period. In 1989, the focal colony was abandoned on day 42 (verticle arrow).

Too few cowbird visits were observed in 1990 ($n = 7$) for a similar analysis. The pattern of cowbird visits also differed significantly from random if only the morning visitations are considered ($\chi^2 = 7.14$, df = 2, $P < 0.05$). Pooling data from all years and excluding time blocks with fewer than 5 hr observation, the number of cowbird visits per hour was significantly negatively correlated with the average number of females

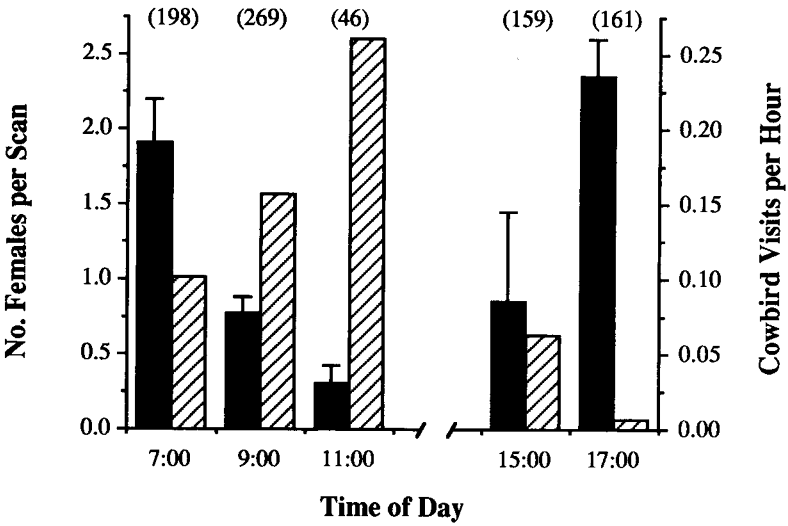

FIGURE 2. Mean number of females perched in the colony during scan samples (solid bars; n = 576 scans [1987] and 829 scans [1988]) and number of cowbird visits to the colony per hour of observation (hatched bars) versus time of day. For number of females present, error bars show 1 standard error. The X-axis gives the midpoint of each 2-hr time block, and numbers in parentheses are the total number of hours of observation in each time block during which cowbird data were collected. The 12:00–14:00 time block was excluded from analyses due to a low number of observation hours (<5).

present in the colony during each time block (Spearman's $\rho = -0.683$, $n = 9$ one-hour time blocks, $P = 0.05$).

Cowbird visits late in the morning appeared to be more successful than visits early in the morning: cowbirds entered nests on only 6.8% of 44 visits before 09:00, but were able to enter nests on 20.0% of 20 visits between 09:00 and 12:00. However, this last result is not statistically significant ($\chi^2 = 2.45$, df = 1, $P > 0.05$), and a larger sample size is needed before firm conclusions can be drawn regarding the success of cowbirds at different times of the day.

DISCUSSION

Unlike some populations of Chestnut-headed Oropendolas and Yellow-rumped Caciques, Montezuma Oropendolas in Costa Rica did not tolerate Giant Cowbirds near their nests. Similarly, Robinson (1988), working in Peru, found that Yellow-rumped Caciques and Russet-backed Oropendolas (*Psarocolius angustifrons*) actively defended their nests against Giant Cowbirds. Giant Cowbirds have apparently evolved strategies to circumvent nest defense by their hosts; in this study, cowbirds visited colonies during those times of the day when hosts were most likely to be absent, a strategy that has been reported for other brood parasites (Davies and Brooke 1988). Cowbirds also raid colonies in groups (Robinson 1988, this study), and appear to lay mimetic eggs (Smith 1968, but see Fleischer and Smith 1992).

These results, combined with those of Robinson (1988), suggest that many populations of oropendolas and caciques actively defend against cowbird parasitism, and that the complex host-parasite mutualism reported by Smith (1968, 1979) is likely to be quite rare. There are at least two possible reasons why such a mutualism might have evolved with one host population but not another. First, the benefits to the host might be lower in Costa Rica and Peru than in Panama. This explanation seems unlikely for Montezuma Oropendolas, as botflies appear to frequently parasitize Montezuma Oropendola nestlings; botfly larvae were evident on four of nine young (featherless) nestlings examined during this study (range = 1–16 bots per nestling). Furthermore, Montezuma Oropendolas do not nest in association with social hymenoptera (Fraga 1989), and therefore have no apparent defenses against botfly parasitism (see Smith 1968, 1979, 1983). Alternatively, the costs of interspecific brood parasitism to the host might be high for Montezuma Oropendolas in Costa Rica. Although it requires further testing, this explanation seems more likely: Montezuma Oropendolas have low nesting success (less than one-third of all nests built fledge young) and, although the clutch size is two eggs, females rarely fledge more than a single young (Webster 1994). Therefore, it seems unlikely that a Montezuma Oropendola female could successfully fledge her own young if she also had to raise a cowbird nestling (see also Robinson 1988).

Montezuma Oropendolas appear to have few defenses against cowbirds other than aggression and, possibly, removal of cowbird eggs. However, the clustered dispersion of nests within Montezuma Oropendola colonies (Fraga 1989, Webster 1994) might function, in part, to protect nests from cowbird brood parasitism. Nests in clusters should be better guarded from cowbird attack, because cowbirds are more likely to pass near occupied nests (and be chased out) when approaching nests in clusters than when approaching isolated nests. The data reported here give some support to this hypothesis; a female oropendola was unlikely to chase a cowbird unless it approached her own nest, and cowbirds sometimes were not chased from colonies until they approached a nesting cluster. Other studies have also suggested that aggregated nesting and reproductive synchrony could reduce the costs of cowbird parasitism (Clark and Robertson 1979, Robertson and Norman 1977, Wiley and Wiley 1980). If so, then variation in the degree of nest clustering among species of oropendola and cacique might reflect variation in the degree of cowbird parasitism.

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