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## HOST SELECTION BY THE SHINY COWBIRD UNIVERSITY OF IDAHO

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**Abstract.** Factors important in Shiny Cowbird (*Molothrus bonariensis*) host selection were examined within the mangrove community in Puerto Rico. Cowbirds did not parasitize birds in proportion to their abundance. The cowbird breeding season coincided with those of its major hosts, which were "high-quality" foster species (i.e., species that fledge  $\geq 55\%$  of cowbirds hatched: Yellow Warbler, *Dendroica petechia*; Yellow-shouldered Blackbird, *Agelaius xanthomus*; Black-whiskered Vireo, *Vireo altiloquus*; Black-cowled Oriole, *Icterus dominicensis*; Puerto Rican Flycatcher, *Myiarchus antillarum*; Troupial, *Icterus icterus*), and did not extend into other periods even though nests of "low-quality" species (i.e., species that fledge  $< 55\%$  of cowbird chicks that hatched: Bronze Mannikin, *Lonchura cucullata*; Greater Antillean Grackle, *Quiscalus niger*; Gray Kingbird, *Tyrannus dominicensis*; Northern Mockingbird, *Mimus polyglottos*; Red-legged Thrush, *Turdus plumbeus*) were available. Shiny Cowbird food habits and egg size were similar to those of their hosts, suggesting that cowbirds choose hosts partly on the basis of this combination. Cowbirds located host nests primarily by cryptically watching activities of birds in likely habitats. Other nest locating strategies were active searching of suitable habitat and "flushing" of hosts by the cowbird's noisy approach. Cowbirds used nest building and territorial defense activities of hosts as cues to nest location and status. Cowbirds closely monitored nest status with frequent visits that peaked on the host's first day of egg laying. Hosts using covered nests (e.g., cavities, domed nests) were as vulnerable to cowbird parasitism as those building open nests.

**Key words:** *Shiny Cowbird*; *Molothrus bonariensis*; *host selection*; *brood parasitism*; *Puerto Rico*.

### INTRODUCTION

The Shiny Cowbird (*Molothrus bonariensis*) has been expanding its range northward through the West Indies in response to favorable changes in habitat resulting from man's conversion of forests to grazing and agricultural lands (Post and Wiley 1977). This range expansion is analogous to that of the Brown-headed Cowbird (*Molothrus ater*), which has expanded eastward through North America in response to human-related habitat alterations and has exploited naive host populations (Mayfield 1965).

The Shiny Cowbird is an obligate brood par-

asite that uses a generalist strategy in host selection; more than 180 host species have been recorded for the parasite (Friedmann et al. 1977, Mason 1980, Manolis 1982, Wiley 1985). The cowbird probably arrived in Puerto Rico in the late 1940s (Post and Wiley 1977). Local avian populations had no recent history of avian brood parasitism; therefore, it could be predicted that such populations would be quite vulnerable as cowbird hosts. Between 1975 and 1981 I examined host-cowbird relations in Puerto Rico. Whereas I found that many species were not parasitized by the Shiny Cowbird, 11 species were exploited to some degree and all nests of two of these species (Troupial, *Icterus icterus*, and Black-cowled Oriole, *I. dominicensis*) were parasitized (Wiley 1985). Here I describe factors involved in host selection by the Shiny Cowbird.

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Several factors may be important in the Shiny Cowbird's selection of hosts from the array of species and individuals in an avian community, including (1) abundance of the potential host (Friedmann 1963, 1971; Lack 1963; Friedmann et al. 1977), (2) timing of breeding by host and parasite, (3) similarity of food habits between host and cowbird (Friedmann 1963, Rothstein 1976, Mason 1986), (4) similarity of host and parasite egg sizes, (5) the ability of the cowbird to locate the host's nest and monitor host activity there, and (6) the suitability of a host's nest structure.

I made the following predictions of host use by Shiny Cowbirds in my study areas: (1) Shiny Cowbirds would use a host in proportion to its relative abundance in the Puerto Rican community. (2) Cowbird reproductive activity would coincide with that period when the "best" host species were nesting. (3) Shiny Cowbirds would selectively parasitize species on the basis of their food habits. (4) Host egg size would be an important determinant in the selection of host species by the Shiny Cowbird. (5) Cowbirds would use a cryptic watching technique for locating potential host nests more often than other nest locating strategies. (6) Species with open nests should be more vulnerable to parasitism than species using covered structures (e.g., cavities, domed nests). In this paper, I present observations and results of tests based on these predictions.

## METHODS

### STUDY AREAS

Roosevelt Roads Naval Station, my major study area, consists of 3,260 ha at the easternmost point of Puerto Rico about 60 km east of San Juan. Mangrove (black-mangrove, *Avicennia germinans*; white-mangrove, *Laguncularia racemosa*; button-mangrove, *Conocarpus erectus*; and red-mangrove, *Rhizophora mangle*) forests dominate the extensive tidal lands and account for about 25% (814 ha) of the station's land area. There are also level, alluvial valleys, and low hills that are vegetated with grasses, various scrubs, and successional stages between the two.

The Commonwealth Boquerón Forest, my second study site, lies along the southwestern coast of Puerto Rico between Bahía Sucia and Bahía Montalva. It has a red-mangrove fringe, interior black-mangrove forest, and salt flats. Ewel

and Whitmore (1973) characterized both study areas as within the Subtropical Dry Forest Zone although, at a mean of 68 cm per year, annual precipitation at Boquerón Forest is less than half that at Roosevelt Roads. Most rainfall occurs during May and August through November at both study areas.

Wiley (1985) and Wiley and Wiley (1979) give more detailed descriptions of the study areas.

### OBSERVATIONS

I determined the array of hosts available to the cowbird by surveys. Avian population densities were obtained by converting transect counts to absolute values through applying locally determined detectability coefficients based on the lateral distribution patterns of detectable cues (Emlen 1971, 1977). Two transect routes (OC, 1.0 km and LT, 1.1 km in length) were established at Roosevelt Roads in mangrove/salt flat habitat. All counts were started 0.5 hr after local sunrise and continued for 1.0 to 1.3 hr. Routes were covered at weekly intervals through the breeding season (March to June) for a total of 25 surveys.

Towers (3.3 to 5 m tall) were erected at sites that overlooked nesting habitat. I chose nests for observations from among several available for selected species based on suitability (e.g., visibility, potential for disturbance to vegetation; Table 1). Some nests of the various species (e.g., American Kestrel, *Falco sparverius*; columbids; Gray Kingbird, *Tyrannus dominicensis*; Yellow-shouldered Blackbird, *Agelaius xanthomus*) were watched as part of other investigations. Blinds were positioned 2 to 4 m from, and on a level with, or slightly above, bird nests. I used 10 × 40 binoculars and a 15 to 60× zoom spotting scope to make observations. Narrative notes were written or spoken into a portable tape recorder and transcribed later. I scored behavior observations on data forms on which host and cowbird activities had been categorized. From casual observations made during other investigations, I determined most nest searching and egg laying by cowbirds occur in the early morning; therefore, I concentrated observations at nests from dawn through the morning. Assistants and I spent 1,582 hr observing nesting behavior from blinds.

I defined a nest as active when the resident laid at least one egg or, if parasitized and no host egg was laid, when the host incubated the cowbird egg(s). A nest from which one or more chicks

TABLE 1. Hours of observation at nests during egg-laying and early incubation periods, number of Shiny Cowbird visits to nests, and percent of nests parasitized at 106 nests of 27 species of birds, Roosevelt Roads Naval Station, Puerto Rico.

Species <sup>a</sup>	No. nests watched	No. hr. observation	No. visits	No. visits/hr	Percent nests parasitized <sup>b</sup>
Least Bittern	2	13	2	0.15	0
American Kestrel	5	208	0	—	0
White-crowned Pigeon	10	599	11	0.02	0
Zenaida Dove	2	10	1	0.10	0
White-winged Dove	5	46	3	0.07	0
Common Ground-Dove	11	217	3	0.01	0
Yellow-billed Cuckoo	1	8	0	—	0
Mangrove Cuckoo	1	12	0	—	0
Green-throated Carib	2	9	0	—	0
Antillean Crested Hummingbird	1	3	0	—	0
Caribbean Elaenia	2	10	4	0.40	0
Puerto Rican Flycatcher	2	11	10	0.91	85
Gray Kingbird	6	19	0	—	1
Caribbean Martin	2	6	4	0.67	0
Northern Mockingbird	2	9	2	0.22	3
Pearly-eyed Thrasher	9	205	7	0.03	0
Red-legged Thrush	1	18	9	0.50	4
Black-whiskered Vireo	3	13	12	0.92	82
Bananaquit	4	12	1	0.08	0
Yellow Warbler	6	36	38	1.06	76
Yellow-shouldered Blackbird	10	42	114	2.71	95
Greater Antillean Grackle	7	21	8	0.38	11
Black-cowled Oriole	4	16	22	1.38	100
Troupial	1	6	7	1.17	100
Stripe-headed Tanager	2	21	16	0.76	0
Bronze Mannikin	3	6	2	0.33	17
Nutmeg Mannikin	1	3	1	0.33	0
Black-faced Grassquit	1	3	1	0.33	0

<sup>a</sup> Scientific names: Least Bittern (*Ixobrychus exilis*), American Kestrel (*Falco sparverius*), White-crowned Pigeon (*Columba leucocephala*), Zenaida Dove (*Zenaida aurita*), White-winged Dove (*Zenaida asiatica*), Common Ground-Dove (*Columbina passerina*), Yellow-billed Cuckoo (*Coccyzus americanus*), Mangrove Cuckoo (*C. minor*), Green-throated Carib (*Eulampis holosericeus*), Antillean Crested Hummingbird (*Orthorhynchus cristatus*), Caribbean Elaenia (*Elaenia martinica*), Puerto Rican Flycatcher (*Myiarchus antillarum*), Gray Kingbird (*Tyrannus dominicensis*), Caribbean Martin (*Progne dominicensis*), Northern Mockingbird (*Mimus polyglottos*), Pearly-eyed Thrasher (*Margarops fuscatus*), Red-legged Thrush (*Turdus plumbeus*), Black-whiskered Vireo (*Vireo altiloquus*), Bananaquit (*Coereba flaveola*), Yellow Warbler (*Dendroica petechia*), Yellow-shouldered Blackbird (*Agelaius xanthomus*), Greater Antillean Grackle (*Quiscalus niger*), Black-cowled Oriole (*Icterus dominicensis*), Troupial (*Icterus icterus*), Stripe-headed Tanager (*Spindalis zena*), Bronze Mannikin (*Lonchura cucullata*), Nutmeg Mannikin (*Lonchura punctulata*), Black-faced Grassquit (*Tiaris bicolor*).

<sup>b</sup> Includes nests not closely watched from blinds.

fledged (either host or parasite) was considered successful.

I captured 2,394 cowbirds in mist nets or in 2-m high walk-in traps placed at feeding sites and in social areas. Traps were baited with cracked corn and other grains, and cowbirds trapped on the previous day were used as decoys. I inspected traps at least twice daily. Mist nets were set in feeding areas where cowbirds congregated before flying to social areas. Captured birds were weighed with spring scales to the nearest 0.5 g, measured with dial or vernier calipers to the nearest 0.1 mm, and checked for molt, disease, and external parasites. All birds were marked with U.S. Fish and Wildlife Service leg bands and a unique combination of three colored celluloid leg bands. Length and width of eggs were measured to the nearest 0.1 mm with vernier or dial calipers.

## EXPERIMENTS

To examine mechanisms cowbirds used in locating host nests, I placed fresh, lined nests of Yellow Warblers (*Dendroica petechia*), Greater Antillean Grackles (*Quiscalus niger*), and Yellow-shouldered Blackbirds about 15 m apart in a grid pattern on a site adjacent to the main Roosevelt Roads study area. In 1979, 25 empty nests were set out in an alternating pattern with 25 nests containing intact host eggs or host eggs blown and filled with gelatin. Eggs were added to the nests at a rate of one per day for 3 days to simulate host laying patterns. In 1980, 27 empty nests and 24 nests with eggs were positioned as in 1979. An additional 25 nests were established with eggs and a mounted or wooden dummy host placed on a conspicuous perch 0.5

m from the nest. In 1981, 29 empty nests, 26 nests with eggs, and 30 nests with eggs and dummy host were positioned on the grid. Nests were inspected daily during the 2-week experiments. I visited empty nests as often as active nests.

#### ANALYSIS

I followed statistical methods as presented by Hollander and Wolfe (1973) and Zar (1975). Significance level was set at 0.05. When the underlying assumptions (e.g., normality, equal variance) were not violated, or only slightly so, I used parametric statistical methods to test for sample differences. In other cases I applied nonparametric statistics for those tests.

#### RESULTS

##### AVIAN POPULATIONS IN THE MANGROVE COMMUNITY

I determined bird densities and numbers of territories at the Roosevelt Roads study area (Table 2). I transformed territory density into abundance of nests available to cowbirds, which is a more important aspect of host availability than numbers of individuals per unit area.

Several species that are known from the naval station were not detected during the surveys. Cave Swallows (*Hirundo fulva*) and Caribbean Martins (*Progne dominicensis*) were not included in the surveys although both were regularly seen using the airspace above the transects. American Kestrels, Puerto Rican Bullfinches (*Loxigilla portoricensis*), Mourning Doves (*Zenaida macroura*), Puerto Rican Screech-Owls (*Otus nudipes*), and Yellow-billed Cuckoos (*Coccyzus americanus*) breed in the Roosevelt Roads mangrove habitat, but I did not detect them during my surveys. Nests of these species were inspected, but none contained cowbird eggs.

I found no association between species abundance and degree of parasitism (Tables 1 and 2; see Wiley 1985 for parasitism rates). Percentage of nests parasitized in the OC avian community was not correlated with the abundance of all nesting species, only passerines, or with the abundance of only parasitized species (product-moment correlation coefficient,  $r = 0.34, 0.39,$  and  $0.27,$  respectively;  $P > 0.05,$   $t$ -test). I obtained comparable results for the LT avian community ( $r = 0.19$  for relationship of all breeding species abundance and degree of parasitism;  $r = 0.002$  for only passerines, and  $r = 0.03$  for only parasitized species;  $P > 0.05$ ).

Although my estimates of bird densities may be flawed by several sampling problems, I believe the relative abundance of species in the mangrove community is accurately represented. Thus the lack of relationship between nesting species abundance (i.e., number of nests available) and proportion of nests parasitized is probably real.

#### BREEDING CHRONOLOGY

Although some species (e.g., Greater Antillean Grackles; Bananaquit, *Coereba flaveola*) breed throughout the year in Puerto Rico, most passerines confine their reproductive activity to the spring and summer (Fig. 1). The main breeding season at Roosevelt Roads began in late March, which corresponded with the onset of increased precipitation in eastern Puerto Rico (Fig. 2). Egg-laying activity at the Boquerón study area began several weeks after activity commenced at Roosevelt Roads, possibly due to the delayed start of the wet season in southwestern Puerto Rico (Fig. 3).

I determined the initiation of cowbird breeding activity by observing cowbird eggs in nests and by monitoring female cowbird weight gains related to egg production. Female cowbirds began gaining weight in early March ( $\bar{x} = 31.7 \pm 2.90$  [SD] g,  $n = 111$ ), which preceded egg laying by major hosts by several days. Increases in cowbird weight peaked in mid-June ( $\bar{x} = 33.3 \pm 3.13$  g,  $n = 18$ ), then declined through summer (July:  $\bar{x} = 32.1 \pm 2.51$  g,  $n = 60$ ; August:  $\bar{x} = 32.2 \pm 2.13$  g,  $n = 40$ ). In early September, weights of female cowbirds ( $\bar{x} = 31.0 \pm 1.73$  g,  $n = 33$ ) still were elevated above the pre-March levels (December:  $\bar{x} = 30.6 \pm 2.91$  g,  $n = 44$ ; January:  $\bar{x} = 30.3 \pm 1.94$  g,  $n = 77$ ; February:  $\bar{x} = 30.3 \pm 2.40$  g,  $n = 105$ ); a few hosts were nesting and a few cowbird eggs were found in September. I observed cowbird eggs in the nests of the earliest-laying Yellow Warblers and Yellow-shouldered Blackbirds through to mid-August, when the last individuals of these species laid eggs (Fig. 1).

Although Greater Antillean Grackles nested throughout the year, I did not find parasitized nests beyond the breeding season of high-quality hosts (i.e., species that fledge  $\geq 55\%$  of cowbirds hatched). I considered the grackle a low-quality host (i.e., species that fledge  $< 55\%$  of cowbirds hatched), since cowbird hatching and fledging success were substantially lower at grackle nests than at nests of hosts with higher rates of para-

TABLE 2. Summary of 25 surveys of birds along 1.0- and 1.1-km routes at two mangrove communities (OC and LT study areas), Roosevelt Roads Naval Station, eastern Puerto Rico, March through June, 1980 and 1981.

Species <sup>a</sup>	Transect route			
	OC transect		LT transect	
	Mean density 10 ha <sup>b</sup>	Territories/ 100-m strip <sup>c</sup>	Mean density 10 ha <sup>b</sup>	Territories/ 100-m strip <sup>c</sup>
White-crowned Pigeon	1.6	5	1.6	4
Zenaida Dove	1.9	5	4.7	8
White-winged Dove	2.4	10	1.2	5
Common Ground-Dove	3.4	6	3.8	6
Mangrove Cuckoo	2.0	1	1.4	2
Puerto Rican Lizard-Cuckoo	0.1	1		
Smooth-billed Ani	0.7	2	1.6	1
Green-throated Carib	10.0	8	8.5	5
Antillean Crested Hummingbird	2.5	2	1.8	2
Caribbean Elaenia	2.2	11	1.3	3
Gray Kingbird	6.3	12	5.4	7
Northern Mockingbird	0.7	5	1.6	6
Pearly-eyed Thrasher	0.1	1		
Red-legged Thrush	1.3	1		
Black-whiskered Vireo	1.0	1	0.3	1
Bananaquit	5.8	12	11.8	12
Northern Parula	1.5		0.5	
Yellow Warbler	26.2	42	18.9	30
Palm Warbler	2.3		1.5	
Ovenbird	1.0		1.0	
Northern Waterthrush	16.7		0.3	
Yellow-shouldered Blackbird	10.0	5		
Black-cowled Oriole	0.6	1	0.5	1
Greater Antillean Grackle	4.3	8	2.1	6
Shiny Cowbird	3.2		1.5	
Stripe-headed Tanager	3.0	1	2.5	2
Bronze Mannikin	1.0	1		
Nutmeg Mannikin	3.8	8	2.2	3
Black-faced Grassquit	0.5	1	15.5	10

<sup>a</sup> Scientific names of species not listed in Table 1: Puerto Rican Lizard-Cuckoo (*Saurothera vieilloti*), Smooth-billed Ani (*Crotophaga ani*), Northern Parula (*Parula americana*), Palm Warbler (*Dendroica palmarum*), Ovenbird (*Seiurus aurocapillus*), Northern Waterthrush (*Seiurus noveboracensis*), Shiny Cowbird (*Molothrus bonariensis*).

<sup>b</sup> All birds detected by sightings, calls, or songs within the specific strip and projected to 10-ha area.

<sup>c</sup> Sum of whole or fractional territories as determined by clusters of points representing song sites within 100 m of trail on date when species population was at maximum. 100-m strip = 10 ha.

sitism; cowbird hatching success at grackle nests was 15%, as compared to 39% ( $\bar{x}$  for four species) for high-quality hosts, and cowbird fledging success (chicks/cowbird egg) at grackle nests was 8%, as compared to 26% at nests of high-quality hosts (Wiley 1985).

#### SIMILARITY OF FOOD HABITS

I have summarized the breeding season food habits of the Shiny Cowbird and its actual and potential hosts in the two Puerto Rico study areas (Table 3). Of the 11 species I recorded as parasitized by the Shiny Cowbird (Table 3; Wiley 1985), the seed-eating Bronze Mannikin (*Lonchura cucullata*) had the narrowest feeding overlap with the parasite. Although the diet of adult cowbirds includes seeds of various grasses, I suspect this diet would be inadequate to sustain

cowbird chicks. Unfortunately, the cowbird egg did not hatch at the single parasitized Bronze Mannikin nest so development of the seed-fed cowbird chick could not be evaluated. Several other graminivores (Nutmeg Mannikin, *Lonchura punctulata*; Black-faced Grassquit, *Tiaris bicolor*; Yellow-faced Grassquit, *T. olivacea*) were not parasitized (Table 3).

None of the several columbids, nor any of the primarily nectarivorous (e.g., Bananaquit, hummingbirds) or frugivorous (Stripe-headed Tanager, *Spindalis zena*) species were parasitized on the study areas. I found no parasitized nests of birds that fed primarily on large invertebrates or small vertebrates (cuckoos; Pearly-eyed Thrasher, *Margarops fuscatus*).

There was broad feeding niche overlap among cowbirds and the remaining 12 species in my

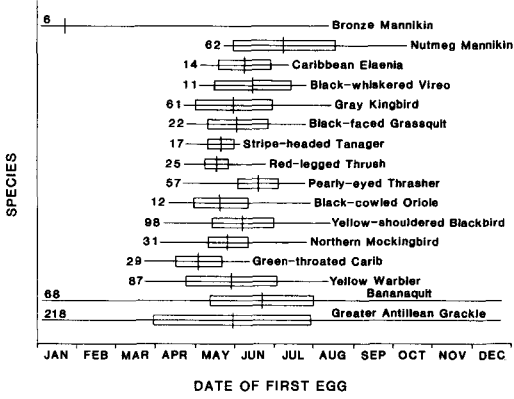


FIGURE 1. Timing of egg laying for 16 species in a mangrove community at Roosevelt Roads Naval Station, eastern Puerto Rico, 1975 to 1981. Vertical line represents mean egg-laying date, horizontal line represents the range of egg-laying dates, and the open box represents one standard deviation about the mean. Number of nests examined is given at left of range line.

study areas. I found that 83% ( $n = 10$ ) of these species were parasitized to some degree, and 58% (7) were successfully parasitized (i.e., fledged cowbirds; Wiley 1985).

Species with adult-to-chick food-passing behavior different from typical passerine mechanisms were not parasitized. Food exchange between adult and nestling columbids and mannikins (Nicolai 1964) requires special structural and behavioral adaptations, so it is unlikely that cowbird chicks could duplicate these feeding mechanics. Similarly, the special mechanisms for food exchange between hummingbird adults and chicks preclude successful parasitism of that group.

EGG SIZE

Egg sizes of potential hosts at the Puerto Rico study areas spanned a wide range (Table 3). I found that host eggs often were at the upper or lower limits of the parasite's egg-size range (e.g., Yellow Warbler, Greater Antillean Grackle), but only one occasionally used host species (Red-legged Thrush, *Turdus plumbeus*) was outside that range. Thus, the hypothesis of egg-size similarity among hosts of the Shiny Cowbird is upheld. However, I performed no experiments on egg size, and only present data on correlations. Therefore, the association between egg size and parasitism may be only a spurious correlation and the important factor may be similarity in diet or in size of the host species.

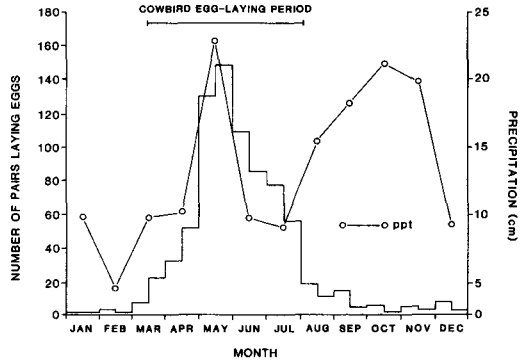


FIGURE 2. Mean number of birds of 16 species laying eggs per 2-week period at Roosevelt Roads Naval Station, eastern Puerto Rico, 1975 to 1981. Mean monthly precipitation at the Fajardo Station (6 km west of naval station) is plotted with open circles connected by line.

SHINY COWBIRD MECHANISMS FOR LOCATING AND SELECTING HOST NESTS

I indirectly tested the prediction that Shiny Cowbirds used a cryptic watching strategy to locate nests of potential hosts by placing Yellow Warbler, Greater Antillean Grackle, and Yellow-shouldered Blackbird nests in suitable habitat at Roosevelt Roads and monitoring these for incidence of cowbird parasitism. None of the empty nests was parasitized, whereas nests in which

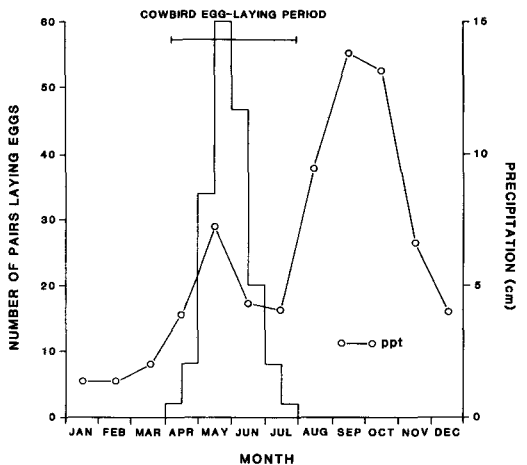


FIGURE 3. Mean number of birds of seven species laying eggs per 2-week period at the Boquerón Forest study area, southwestern Puerto Rico, 1977 to 1980. Monthly precipitation averages from Magüeyes Island Station (at east end of study area) are plotted as open circles connected by line.

host eggs were artificially added and nests with host dummies plus eggs had a low rate of parasitism (Table 4). The incidence of parasitism of empty nests was not different from that of nests with eggs or with dummies and eggs ( $\chi^2 = 4.51$ ,  $df = 2$ ,  $P > 0.05$ ). However, fewer empty nests were parasitized than nests with signs of host activity (egg, dummy host + eggs;  $\chi^2 = 4.51$ ,  $df = 1$ ,  $P < 0.05$ ). Parasitism rates at nests with conspicuous host dummies were not different from nests where only eggs were present ( $\chi^2 = 0.001$ ,  $P > 0.05$ ). Parasitism rates at active control nests of warblers, blackbirds, and grackles ( $n = 271$ ) differed from the collective rate at all experimental nests ( $\chi^2 = 324.2$ ,  $P \ll 0.001$ ), the rate at empty experimental nests ( $\chi^2 = 206.0$ ,  $P \ll 0.001$ ), and the incidence at experimental nests with indirect evidence of cowbird activity ( $\chi^2 = 237.5$ ,  $P \ll 0.001$ ). Thus, host activity was apparently an important factor in cowbird selection of nests.

Cowbirds occasionally lay in empty, inactive nests. I observed six such incidents (three blackbird and three grackle nests) at nests ranging from those built but abandoned without eggs 1 week before the cowbird's laying to one that had been inactive for 5 weeks before being parasitized. All nests retained at least some lining material at the time they were parasitized.

I saw cowbirds watching the activities of prospective hosts to locate nests in 72.1% ( $n = 49$ ) of my observations of cowbird activities before their nest inspections. Cowbirds used perches in suitable nesting habitat to maintain vigilance of breeding bird activity. These perches averaged  $9.4 \pm 0.59$  m (range = 2–23 m,  $n = 49$  observations) from the host nest they visited. Besides this silent vigilance, I observed cowbirds using two other strategies to locate host nests: (1) active searches and (2) "flushing" behavior. Active searches involved female cowbirds quietly moving through nesting habitat in short flights and hops through dense, interior vegetation. Often these movements were in the company of a male and/or one or two females. Active searches for nests accounted for 14.7% ( $n = 10$ ) of my observations of Shiny Cowbird activities before nest inspections. Flushing behavior ( $n = 9$  observations; 13.2%) consisted of a female cowbird making short, noisy flights into prospective nesting areas, apparently in an attempt to flush hosts from their nests. Perhaps these obvious movements also served to arouse defense responses

from nesting birds which thereby revealed nest location.

I observed cowbirds visiting nests of 12 of the 17 unparasitized species I closely watched from blinds (Table 1). Cowbirds were not observed visiting the nests of American Kestrels, Yellow-billed Cuckoos, Mangrove Cuckoos (*Coccyzus minor*), Green-throated Caribs (*Eulampis holosericeus*), Antillean Crested Hummingbirds (*Orthorhynchus cristatus*), or Gray Kingbirds (Table 1).

Rates of cowbird visits to nests of unparasitized and low-quality host species averaged lower than at nests of high-quality species:  $1.35 \pm 0.68$  cowbird visits per hour at nests of high-quality hosts ( $n = 6$  species; range = 0.91–2.71/hr);  $0.19 \pm 0.23$  per hour at nests of low-quality hosts or nonparasitized species ( $n = 22$  species; range = 0–0.76/hr; Fisher-Behrens  $t$ -test,  $t = 4.081$ ,  $P < 0.01$ ). The rate of cowbird visits to nests of only low-quality or unparasitized passerines averaged higher ( $0.34 \pm 0.24$  visits/hr; range = 0–0.76/hr;  $n = 12$  species) than all nonparasitized and low-quality species, but was still lower than the rate at nests of high-quality hosts (all passerines;  $t = 3.538$ ,  $P < 0.02$ ). The rate of cowbird visitations to nests of various species was correlated with the degree of parasitism among the species (Spearman's rank correlation coefficient,  $r_s = 0.698$  for all species,  $df = 27$ ;  $r_s = 0.698$  for passerines only,  $df = 17$ ; both  $P < 0.01$ ).

I recorded eight categories of host behavior performed before female cowbirds visited nests. Nest building (delivery of nest material—22.2%,  $n = 14$  observations; nest construction—14.3%,  $n = 9$ ) was the most common activity before cowbird inspections. Territorial defense (including vocal defense) against conspecifics and other species was also a frequent activity (30.2%,  $n = 19$ ) of hosts before cowbird nest visits. Often distant cowbirds quickly moved into areas where residents were defending against intruders, suggesting that the cowbirds used the residents' defense vocalizations as a cue. Other activities included foraging (12.7%,  $n = 4$ ), incubation (11.1%,  $n = 7$ ), loafing (6.3%,  $n = 4$ ), nest exchange (1.6%,  $n = 1$ ), and vigilance (1.6%).

Cowbirds visited nests from 0.03 to 29.0 min ( $\bar{x} = 6.34 \pm 1.02$  min,  $n = 57$ ) after hosts left their nests. Hosts averaged short attendance periods ( $\bar{x} = 3.75 \pm 0.99$  min, range = 0–26.0 min;  $n = 46$ ) at nests before they left and cowbirds made inspection visits.

TABLE 3. Breeding season food habits, egg dimensions and type of nest structures of birds at Roosevelt Roads Naval Station and Boquerón Forest study areas, Puerto Rico.

Species <sup>a</sup>	Percent nests parasitized (n)	Diet <sup>b</sup>	Egg measurements (mm)			Type of nest
			No.	Length	Breadth	
Tricolor Heron	0 (153)	Small fish [1]	8	45.18 ± 0.64	33.36 ± 0.49	Open
Least Bittern	0 (61)	Small fish, invertebrates [1]	28	31.37 ± 0.35	24.17 ± 0.10	Open
White-cheeked Pintail	0 (8)	Grass seeds, algae, invertebrates [1]	25	50.92 ± 0.33	35.46 ± 0.67	Open
Clapper Rail	0 (98)	Crustaceans, mollusks, small fish [1]	61	42.37 ± 0.33	13.04 ± 0.07	Open
Black-necked Stilt	0 (181)	Invertebrates, small fish [1]	76	43.10 ± 0.29	31.14 ± 0.15	Open
Common Moorhen	0 (122)	Invertebrates, vegetation [1]	7	44.70 ± 0.47	31.42 ± 0.14	Open
Least Tern	0 (77)	Small fish [2]	8	32.26 ± 0.24	23.01 ± 0.23	Open
Wilson's Plover	0 (133)	Invertebrates [2]	24	35.97 ± 0.17	26.51 ± 0.13	Open
White-crowned Pigeon	0 (373)	Fruits, seeds <sup>c</sup> [3]	88	36.20 ± 0.08	26.10 ± 0.05	Open
Zenaida Dove	0 (417)	Seeds, (fruits) <sup>b</sup> [1, 2]	6	29.53 ± 0.42	22.03 ± 0.08	Open
Mourning Dove	0 (17)	Seeds, fruits <sup>c</sup> [2]				Open
White-winged Dove	0 (271)	Fruits, seeds <sup>c</sup> [2]				Open
Common Ground-Dove	0 (411)	Seeds <sup>c</sup> [1]	25	29.73 ± 0.19	22.72 ± 0.22	Open
Mangrove Cuckoo	0 (5)	Large insects [1]	23	21.83 ± 0.14	16.70 ± 0.18	Open
Puerto Rican Lizard-Cuckoo	0 (3)	Lizards, large invertebrates [1]	1	32.2	23.2	Open
Smooth-billed Ani	0 (12)	Large arthropods [1]				Open
Antillean Nighthawk	0 (16)	Insects [2]	1	27.7	21.2	Open
Green-throated Carib	0 (29)	Small arthropods, nectar [1]	3	14.00 ± 0.35	9.33 ± 0.09	Open
Antillean Crested Hummingbird	0 (13)	Nectar, small arthropods [1]				Open
Caribbean Elaenia	0 (14)	Seeds, fruits, arthropods [1]	3	20.63 ± 0.58	16.03 ± 0.48	Open
Puerto Rican Flycatcher	85 (13)	Arthropods, (seeds) [1]	12	21.02 ± 0.23	15.93 ± 0.11	Cavity <sup>d</sup>
Gray Kingbird	1 (76)	Large insects, fruits, seeds [1]	25	24.88 ± 0.41	18.48 ± 0.36	Open
Caribbean Martin	0 (7)	Insects [1]				Cavity <sup>d</sup>
Northern Mockingbird	3 (44)	Fruits, large insects [1]	3	26.15 ± 0.62	18.63 ± 0.39	Open
Pearly-eyed Thrasher	0 (57)	Large arthropods, small lower vertebrates [1, 2]	2	31.85 ± 0.75	22.05 ± 0.05	Cavity <sup>d</sup>
Red-legged Thrush	4 (25)	Fruits, seeds, arthropods, small lower vertebrates [1]	6	29.48 ± 0.24	22.40 ± 0.10	Open
Black-whiskered Vireo	82 (11)	Fruits, insects, small amphibians [1]	4	22.20 ± 0.30	15.30 ± 0.23	Open
Bananquit	0 (90)	Nectar, small insects [1]	3	18.77 ± 0.41	12.93 ± 0.36	Domed
Yellow Warbler	76 (107)	Insects [1]	37	15.57 ± 0.11	13.45 ± 0.06	Open
Yellow-shouldered Blackbird	95 (164)	Insects, seeds, nectar [1, 2]	59	22.69 ± 0.14	16.75 ± 0.10	Open (n = 131)
Shiny Cowbird		Seeds, insects [2, 4, 5]	235	20.65 ± 0.06	16.46 ± 0.04	Cavity <sup>d</sup> (n = 33)
Troupial	100 (5)	Fruits, arthropods [4]				Pendulant
Black-cowled Oriole	100 (12)	Arthropods, nectar, small lower vertebrates [1]	3	24.33 ± 0.18	17.57 ± 0.09	Attached under leaf



TABLE 3. Continued.

Species <sup>a</sup>	Percent nests parasitized (n)	Diet <sup>b</sup>	Egg measurements (mm)			Type of nest
			No.	Length	Breadth	
Greater Antillean Grackle	11 (218)	Arthropods, small lower vertebrates [1, 2]	197	27.09 ± 0.09	19.73 ± 0.05	Open
Stripe-headed Tanager	0 (17)	Fruit [1, 2]	3	23.03 ± 0.17	16.40 ± 0.07	Open
Bronze Mannikin	17 (6)	Grass seeds [6]	16	15.98 ± 0.21	11.26 ± 0.06	Domed
Nutmeg Mannikin	0 (62)	Grass seeds, berries, insects [4]	45	16.22 ± 0.15	11.42 ± 0.06	Domed
Black-faced Grassquit	0 (22)	Grass seeds [1]	16	16.26 ± 0.23	13.04 ± 0.14	Domed
Warbling Silverbill	0 (13)	Grass seeds [6]	5	15.26 ± 0.51	11.36 ± 0.03	Domed

<sup>a</sup> Scientific names of species not in Tables 1 and 2: Tricolor Heron (*Egretta tricolor*), White-cheeked Pintail (*Anas bahamensis*), Clapper Rail (*Rallus longirostris*), Black-necked Stilt (*Himantopus mexicanus*), Common Moorhen (*Gallinula chloropus*), Least Tern (*Sterna antillarum*), Wilson's Plover (*Charadrius wilsonia*), Mourning Dove (*Zenaidura macroura*), Antillean Nighthawk (*Chordeiles gundlachi*), Warbling Silverbill (*Lonchura malabarica*).

<sup>b</sup> Sources for diet data: [1] Wetmore 1916; [2] Wiley and Wiley 1979; [3] Friedmann 1929; [4] Long 1981; [5] Friedmann 1929; [6] Herbert Raffaele, unpubl. data.

<sup>c</sup> Chicks fed specialized crop milk.

<sup>d</sup> Natural cavities and nest boxes.

TABLE 4. Parasitism experiments at nests of Yellow Warblers, Greater Antillean Grackles, and Yellow-shouldered Blackbirds, Roosevelt Roads Naval Station, eastern Puerto Rico, 1979 to 1981.

Year	Experiment	No. nests	No. nests parasitized	No. cowbird eggs per parasitized nest
1979	Empty nest	25	0	
	Nest with eggs <sup>a</sup>	25	2	1.0
1980	Empty nest	27	0	
	Nest with eggs <sup>a</sup>	24	0	
	Nest with eggs + host model <sup>b</sup>	25	2	1.0
1981	Empty nest	29	0	
	Nest with eggs <sup>a</sup>	26	2	1.0
	Nest with eggs + host model <sup>b</sup>	30	1	1.0

<sup>a</sup> One egg per day added to nest on three consecutive days.

<sup>b</sup> One egg per day added to nest on three consecutive days; model of Yellow-shouldered Blackbird or Yellow Warbler host placed 0.5 m from nest.

Occasionally, cowbirds visited nests while hosts were still present. Despite the intruder's approach to within 3 to 5 cm of the nest, hosts did not always flush from the nest or chase the cowbird but sometimes stayed still and low. Possibly this behavior evolved to conceal and protect the eggs from predators and now also discourages cowbirds from depositing eggs in the host's nest.

Cowbird visits to host nests began during building, gradually increased during pre-egg laying, and reached a peak on the first day of laying for three host species I closely watched (Fig. 4).

From my observations I concluded that cowbirds locate host nests by cryptically watching for direct cues, particularly nest building and territorial defense activities. Parasites closely monitor nest status during the nest-building and egg-laying periods, presumably to synchronize their egg laying with that of their hosts.

#### NEST STRUCTURE

Breeding birds in the two study areas used several types of nest structures, including open, pendulant, canopied (oriole nests stitched to the undersides of leaves), domed, and cavity nests. All nest styles were parasitized (Table 3). There was no difference in the rate of parasitism between these open and covered nests ( $P > 0.05$ , Kolmogorov-Smirnov test).

Yellow-shouldered Blackbirds used cavities (natural and nest boxes) and open nests. Both

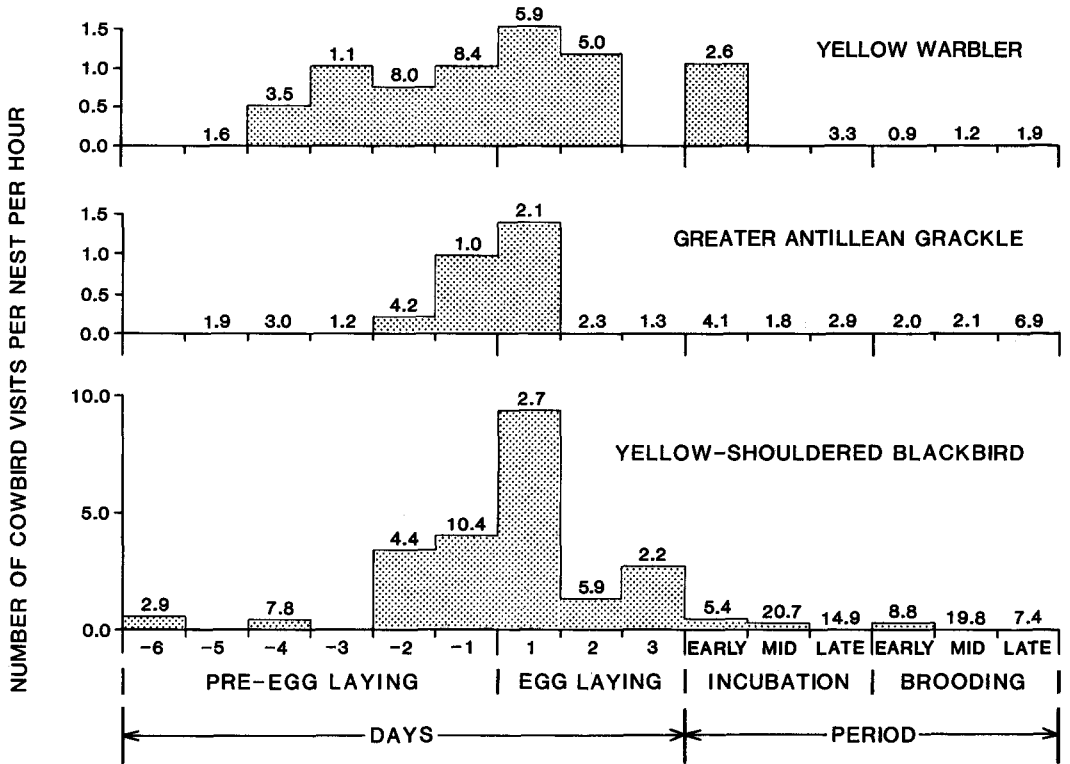


FIGURE 4. Shiny Cowbird prospecting and egg-laying activities at nests of three host species (Yellow Warbler, Yellow-shouldered Blackbird, Greater Antillean Grackle), Roosevelt Roads Naval Station, eastern Puerto Rico. Pre-egg-laying and egg-laying periods are divided into days before (-1, -2, etc.) and days during (1, 2, 3) egg laying. Incubation and brooding are divided into early, mid-, and late periods. Hours of observation for each period are presented above columns. All observation periods began at dawn.

nest types were parasitized at the same rate (98% vs. 93%,  $P < 0.05$ ), and nest success did not differ between cavity nests (37%) and open nests (40%). However, more host chicks fledged per cavity nest than from open nests (open = 0.2 fledged/nest, cavity = 0.5/nest;  $P < 0.001$ ,  $t$ -test). The predation rate at open nests of blackbirds was greater than for cavity nests ( $P < 0.01$ ).

My major findings on Shiny Cowbird host selection were: (1) cowbirds did not parasitize birds in proportion to their abundance. (2) The cowbird breeding season coincided with that of its major hosts, which were high-quality foster species, and did not extend into other seasons even though nests of low-quality hosts were available. (3) Food habits of cowbirds and their major hosts overlapped substantially. (4) Egg size of host and parasite were similar. (5) Cowbirds located nests by cryptically watching potential hosts and then closely monitoring their nest status through frequent visits so as to synchronize

their egg laying. (6) Host nest structure type did not influence cowbird parasitism.

## DISCUSSION

### AVIAN POPULATIONS AND HOST SELECTION

Certain behavioral or ecological characteristics of some birds make them unsuitable as Shiny Cowbird hosts at the onset. For example, those having precocial chicks would not make appropriate foster parents. Predators or species with bodies much larger than the parasite might kill or injure the cowbird. One would not expect a parasite to take such risks often. Thus, I eliminated such species (e.g., kestrel; Puerto Rican Lizard-Cuckoo, *Saurothera vieilloti*) from consideration as potential hosts.

Friedmann et al. (1977) suggested that cowbirds may form search images for common host species in the same manner that some predators are believed to form search images for their most

abundant prey (Tinbergen 1946, Opdam 1979). Formation of search images for certain hosts would, all else being equal, result in higher rates of parasitism for common species than for rare ones. I found no evidence of correlation between nesting species abundance and degree of parasitism. Several other factors collectively influence the suitability and availability of a species as a host. These factors may confound any underlying trend for association of parasitism with abundance of individuals in populations.

"Relatedness" was an important factor in the cowbird's selection of host species. Probably more important than close relationships are the common ecologies, behaviors, sizes, and so forth. All other icterids (blackbird, grackle, Troupial, oriole) were parasitized in my study areas (Table 1). Yellow-shouldered Blackbirds, Troupials, and Black-cowled Orioles had the greatest number of cowbird visits to nests per hour (Table 1) and ranked highest in percent of nests parasitized (Table 3). Also, all six cases of natural parasitism of inactive nests were in icterid nests. Icterids are among the most common hosts of the Shiny Cowbird in South America, Trinidad, and Tobago (Friedmann et al. 1977, Manolis 1982). The remaining hosts in my study area were all passerines.

#### AVIAN BREEDING SEASONS AND HOST SELECTION

Brood parasites synchronize their breeding activity with that of their hosts (Payne 1967, 1973; King 1973; Klaas 1975), with cowbird breeding seasons coinciding with the peak of the nesting of high-quality foster species (Payne 1973). In temperate regions, gonadal activity of foster species is timed by photoperiodism (Farner 1964). Parasite-host breeding synchrony may be mediated by a shared photoperiodic response, with the sight of the nest-building hosts stimulating the final stages of cowbird ovarian activity and ovulation (Payne 1967, 1973). In the tropics, cowbird synchrony with nesting birds may be even more dependent on monitoring host activity, since photoperiodic cues may be less detectable in the tropics than in more northern areas. Breeding seasons of tropical hosts may be more directly attuned to the seasonality of food and nesting sites; e.g., breeding may commence in the rainy season(s), as observed on my study areas (also see Skutch 1976). Cowbird breeding will not commence in temperate or tropical areas

unless essential supplementary information is provided; i.e., nesting activities of hosts, which provide information leading to breeding synchrony (Wingfield 1980, 1983).

In my study areas Shiny Cowbirds were able to sustain reproductive output only during the major hosts' egg-laying seasons (late March through early August), even though low-quality hosts bred throughout the year. The Shiny Cowbird occasionally lays eggs in nests of low-quality hosts during the breeding seasons of its primary hosts, but these may represent miscuing on an inappropriate foster species. Or, in the absence of a high-quality host, it may be better to lay an egg in a low-quality nest than to lay it on the ground. Since using a lower-quality host may not achieve a reproductive payoff commensurate with energy investment, cowbirds may be unable to improve their reproductive output by extending activities beyond the period when the "best" hosts are breeding. Whereas some cowbird chicks might fledge from early or late grackle nests, the costs in egg production (perhaps on low-quality [nonarthropod] food) and risk of injury while attempting to invade the larger species' nest might outweigh benefit derived from the few chicks fledged in the off season.

Temporal shifts in the breeding season could be used by hosts in defense against brood parasitism. Carey (1982) has suggested that Indigo Buntings (*Passerina cyanea*) use delay in breeding as a means of avoiding Brown-headed Cowbird parasitism. Scott (1963) found that late Northern Cardinal (*Cardinalis cardinalis*) nests experienced reduced or no parasitism by Brown-headed Cowbirds. No such effective strategy has yet developed within the host populations I observed in Puerto Rico. These host populations may be closely dependent on the same food and habitat components that Shiny Cowbirds need for reproductive activity so that temporal shifts are not likely to evolve without concomitant shifts by the parasite or, if such shifts occur, fledglings may have a poorer chance of survival than those fledged during the normal season.

In some parts of its range the Yellow-hooded Blackbird (*Agelaius icterocephalus*) has evolved greater breeding synchrony than necessitated by the seasonality of its food supply as an alternative strategy to seasonal shifts in reproductive activity (Wiley and Wiley 1980). This temporal restriction has had the effect of reducing vulnerability to Shiny Cowbird parasitism. This strategy

might be effective for tropical host species with colonial nesting habits, such as the Yellow-shouldered Blackbird, but if a host's breeding season were already bracketed by the parasite's breeding activity, it would achieve little benefit from extending breeding activity at either end of the present season. Moreover, the parasite's breeding season may be less directly constrained by the seasonal availability of food than it is in nesting species in which the parents feed their young; i.e., the emancipated cowbird could more easily adjust its breeding season than could the host species.

#### FOOD HABITS AND HOST SELECTION

Whereas some brood parasites (e.g., viduine finches, Common Cuckoo) are host specialists, Brown-headed and Shiny cowbirds are host generalists and successfully parasitize many species. Brown-headed Cowbird chicks showed similar growth rates among several host species with different feeding habits (Norris 1947), indicating a lack of rigid nutritional constraints. Such food habits adaptability is essential to the generalist strategy of some cowbirds.

Many species in my study areas were unavailable as hosts because of ecological or functional differences in feeding between the adults and cowbird chicks. Only species that fed primarily on insects were parasitized.

#### MECHANISMS FOR LOCATING AND SELECTING HOST NESTS

There is considerable selective advantage for the parasite in closely monitoring host breeding activities. Monitoring of potential host activities may be important to the cowbird in determining the precise time to deposit its egg(s) for the highest probability of acceptance. Parasite eggs deposited too early or after the host completes its clutch are more likely to be rejected, therefore there must be strong selective pressure to synchronize egg laying with the host. My observations showed that Shiny Cowbird visits to host nests peaked during host egg laying. Apparently host activity held some cues to the timing of their laying.

Monitoring of nests also provides the parasite with information on location of the host. Visits to nests while hosts are present may result in injury to the parasite that could be avoided by waiting until the host is seen to leave the nest

area. Monitoring nesting activities also allows the parasite to avoid certain species that are poor hosts or threats as cowbird predators. Shiny Cowbirds made fewer visits to the nests of low-quality and unparasitized species than to nests of high-quality species. Most of the visits to nests of low-quality and unparasitized species were observed on only one occasion. Possibly the cowbirds determined those nests to be unsuitable and did not return for additional inspections or to deposit eggs.

Many workers have reported cowbirds silently watching nesting activities of potential hosts (similar to my observations of "cryptic watching") before the parasites laid their eggs in those nests, and several have suggested that cowbirds use this as a strategy to locate active nests (e.g., Norman and Robertson 1975, Fraga 1978, Gochfeld 1979).

The flushing and systematic searching methods I observed cowbirds using to locate foster nests have also been reported by Norman and Robertson (1975). While these methods are apparently useful in locating nests, subsequent observations of host activities would be needed to obtain information required for egg-laying synchrony. Hence these techniques are probably used to find the nest, but nest selection is the result of cowbirds monitoring nest status by vigilance and occasional visits. Active searching could be dangerous to cowbirds if they encountered a large, aggressive nesting bird during their movements through the vegetation. Flushing and active search nest-location methods are also energy-expensive compared to vigilance and may not be economical strategies.

Cowbirds may cue indirectly on host nesting activities. Cowbird interest in nests containing eggs but without the stimulus of host activity has been demonstrated by Johnston (1957) and King (*in* Norman and Robertson 1975).

Brown-headed and Shiny cowbirds occasionally deposit eggs in unused nests, suggesting that host activity is not essential for nest discovery (Hoy and Ottow 1964, Nolan *in* Thompson and Gottfried 1981, Thompson and Gottfried 1981). Laying in inactive nests should be uncommon if cowbirds are closely monitoring host activities; i.e., cowbirds would thereby know when nests were abandoned. Still, I also observed some cowbirds laying eggs in unused nests. However, earlier activity by hosts may have played a role in the parasites locating these nests as hosts were

observed at some nests only a week before they were parasitized. I also observed considerable stealing of nest material within and among species. This activity at abandoned nests could have been interpreted as building by prospecting cowbirds, resulting in inappropriate parasitism.

Several workers have performed experiments similar to those I conducted to determine nest locating strategies used by cowbirds (Laskey 1950; Thompson and Gottfried 1976, 1981; Lowther 1979). From the results of these experiments, apparently cowbirds rely primarily on observations of host activity in locating appropriate nests.

Activities of hosts before cowbird visits to nests suggest that Shiny Cowbirds may locate nests by vocal cues given by hosts. Gochfeld (1979) found that Shiny Cowbirds used song as a cue in distinguishing suitable hosts and as a clue for finding nesting females at the optimal point in their breeding cycle. Brown-headed and Bronzed (*Molothrus aeneus*) cowbirds may also use alarm calls as cues in locating host nests (Robertson and Norman 1977, Carter 1986).

Host populations may coevolve antiparasite strategies to counter the nest locating activities of cowbirds. For example, individuals may interrupt nest building in the presence of a cowbird and wait until the parasite leaves the area to continue. Hosts may also build surreptitiously to avoid detection by cowbirds. Gochfeld (1979) has observed such strategies among Pampas Meadowlark (*Sturnella defilippii*) populations that are parasitized by Shiny Cowbirds. These strategies may have initially evolved as predator avoidance behaviors but have become adapted as antiparasite mechanisms because of the strong selective value in countering brood parasitism.

#### NEST STRUCTURE

The type of nest structure apparently is not a critical deterrent in preventing Shiny Cowbird parasitism. All forms of nest structures used by hosts in Puerto Rico have been reported as used by Shiny Cowbirds elsewhere; e.g., cavity nest—House Wren, *Troglodytes aedon*; domed nest—Lesser Antillean Bullfinch, *Loxigilla noctis*; pendulant nest—Yellow Oriole, *Icterus nigrogularis*; woven nest stitched to underside of leaf—Martinique Oriole, *I. bonana*, and Moriche Oriole, *I. chrysocephalus* (French 1973). Shiny Cowbirds commonly penetrate structures as complex as the mud-domed, chambered nests of ovenbirds

(Furnariidae; Friedmann 1929). The risk of a cowbird entering the nest of the larger and more aggressive Rufous Hornero (*Furnarius rufus*) must be considerable, yet that species is commonly the victim of multiple parasitism. However, there may be some fitness gain in parasitizing a large, aggressive host in that nests of these species may be less vulnerable to predation.

Parasitizing any covered nest must involve a degree of risk in that the parasite could become trapped in the structure by the host. This could result in physical injury inflicted by a host larger than the cowbird. Such hazards possibly are offset by the advantage of the greater nest success of hosts using cavities and other covered nest structures (Lack 1954). Skutch (1966, 1976) found that nest success of species using holes was nearly twice that of species using open nests in Costa Rica. Cowbird reproductive success may also be greater in cavity nests.

Although I observed no difference in percentage parasitized or success between open and cavity nests of Yellow-shouldered Blackbirds, I found that more host chicks fledged from cavities than open nests. I suspect this difference arises from the lower predation rates (primarily from the Pearly-eyed Thrasher which may affect productivity by removal of one egg or chick without altering nest success) at cavity nests.

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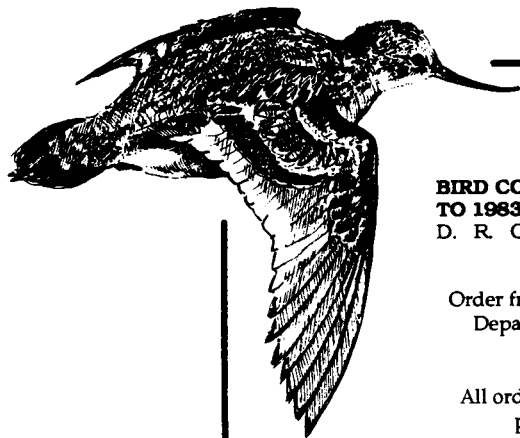
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