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ANTI-BROOD PARASITE STRATEGIES OF NAÏVE POPULATIONS OF NESTING BIRDS IN PUERTO RICO

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Abstract: The Shiny Cowbird (*Molothrus bonariensis*), a generalist brood parasite, arrived in Puerto Rico in the 1940s or early 1950s. No previous record of brood parasites exists for Puerto Rico, so the avian communities had no defenses specialized to counter cowbird parasitism. Nevertheless, some native species were parasitized at high rates, whereas others were able to avoid cowbird parasitism. I examined native bird behaviors that reduced the chance of parasitism, with the prediction that some ecological or behavioral mechanisms used to counter nest depredation may effectively counter parasitism. Certain habitat components (e.g., placement of nests low in dense stands of vegetation) associated with reduced nest depredation may also be effective in concealing nests from brood parasites. Similar to avian populations with long histories of coevolution with brood parasites, the recently exposed populations of nesting birds in Puerto Rico were divided into discrete categories of acceptors and rejectors of alien eggs. Regularly parasitized species were characteristically acceptors, whereas species with low rates of nest parasitism were rejectors. Nest guarding is an effective strategy in countering brood parasitism. Species displaying high nest attentiveness experienced a lower incidence of parasitism than species showing low attendance. Nesting species that were aggressive toward all territory invaders incurred low rates of parasitism. Heavily parasitized species showed lower aggression toward cowbirds than toward other species. Aggressive individuals also incurred lower parasitism rates than did individuals showing lower aggressive responses to nest territory intruders. Individuals of colony-nesting species that nested within colonies incurred lower rates of parasitism than did birds nesting outside the area defended by neighbors. Also, non-aggressive species were afforded some protection against cowbird parasitism by the more vigorous territorial defense of neighboring species. The data reported here are among the earliest collected on Shiny Cowbird-host interactions in Puerto Rico and, as such, can serve as baselines against which changes in behavior and ecology can be measured over time.

Key words: aggression, anti-parasite defenses, brood parasitism, egg rejection, habitat selection, host nest defense, *Molothrus bonariensis*, nest guarding, Shiny Cowbird, territory defense, West Indies

Resumen: LAS ESTRATEGIAS ANTI-PARÁSITOS DE NIDADA DE LAS INGENUAS POBLACIONES DE AVES NIDIFICANTES EN PUERTO RICO. *Molothrus bonariensis* es un parásito de nidada generalista que llegó a Puerto Rico en la década de los 1940 o principios de los 1950. No existen registros previos de parásitos de nidada en Puerto Rico por lo que las comunidades de aves no tienen defensas especializadas para contrarrestar el parasitismo de esta especie. Sin embargo, algunas especies nativas tuvieron altas tasas de parasitismo mientras que otras fueron capaces de evitarlo. Examiné las conductas de especies nativas que redujeron la posibilidad de ser parasitadas con la predicción de que algunos mecanismos ecológicos y conductuales utilizados para evitar la depredación de nidos pueden contrarrestar el parasitismo. Determinados componentes del hábitat (ej. ubicación baja de los nidos en sitios densos de vegetación) asociados con una reducida depredación de nidos pueden también ser efectivos en ocultar los nidos a los parásitos de nidada. Similares a las poblaciones de aves con largas historias de coevolución con estos parásitos, las recientemente expuestas poblaciones de aves nidificantes en Puerto Rico fueron divididas en categorías discretas de aceptores y aquellos que rechazan huevos ajenos. Las especies parasitadas regularmente fueron típicamente aceptores mientras que aquellas con bajas tasas de parasitismo de nido fueron del grupo de rechazo. El cuidado del nido es una estrategia efectiva para evitar el parasitismo de nidada. Las especies que muestran una alta atención del nido experimentaron una incidencia más baja de parasitismo que aquellas que mostraron una baja atención. Las especies nidificantes que fueron agresivas con todos los intrusos en su territorio incurrieron en bajas tasas de parasitismo. Las especies altamente parasitadas mostraron ser menos agresivas hacia *Molothrus bonariensis* que hacia otras especies. Individuos agresivos también tuvieron tasas de parasitismo más bajas que aquellos que mostraron respuestas menos agresivas hacia los intrusos en los territorios de los nidos. Los individuos de especies coloniales que nidificaron dentro de las colonias tuvieron tasas más bajas de parasitismo que aquellos que nidificaron fuera de las áreas defendidas por sus vecinos. También a las especies no agresivas les fue concedida cierta protección contra el parasitismo del Pájaro Vaquero por las especies vecinas más fuertes en la defensa del territorio. Los datos registrados aquí están entre los primeros colectados en las interacciones del Pájaro Vaquero-huésped en Puerto Rico y como tal pueden servir como línea base en relación con cuáles cambios conductuales y ecológicos pueden ser medidos en el tiempo.

Palabras clave: agresión, Antillas, Caribe insular, cuidado del nido, defensas anti-parásito, defensa del territorio, defensa del nido del huésped, parasitismo de nidada, rechazo de huevos, *Molothrus bonariensis*, Pájaro Vaquero

Résumé : LES STRATÉGIES DES POPULATIONS INDIGÈNES D'OISEAUX NICHEURS CONTRE LE PARASITISME DE COUVÉE A PORTO RICO. Le Vacher luisant (*Molothrus bonariensis*), une espèce généraliste parasitant les couvées, est arrivé à Porto Rico dans les années quarante ou au début des années cinquante. Il n'existe pas de données antérieures de parasitisme de couvée à Porto Rico, ainsi les communautés d'oiseaux n'avaient pas de défenses pour faire face au Vacher. Toutefois, certaines espèces indigènes étaient fortement touchées alors que d'autres étaient capables d'éviter le parasitisme du Vacher. J'ai examiné des comportements des oiseaux indigènes qui diminuaient les risques de parasitisme, avec l'hypothèse que certains mécanismes écologiques ou comportementaux utilisés pour contrer la prédation des nids pourraient efficacement contrer le parasitisme. Certaines composantes de l'habitat (p. ex. une position basse des nids dans une végétation dense) associées à une faible prédation des nids pourraient également être efficaces pour dissimuler les nids aux oiseaux parasites de couvée. Comme les populations d'oiseaux ayant longuement coévolué avec les espèces parasites de couvée, les populations d'oiseaux nicheurs récemment exposées à ce phénomène à Porto Rico étaient divisées en catégories distinctes acceptant ou rejetant les œufs exogènes. Les espèces régulièrement parasitées les acceptaient de façon caractéristique, alors que les espèces peu parasitées les rejetaient. La surveillance du nid constitue une stratégie efficace dans la lutte contre le parasitisme. Les espèces portant une grande attention à leur nid étaient plus faiblement touchées que les espèces peu présentes. Les espèces nicheuses agressives envers tous les intrus pénétrant sur leur territoire présentaient de faibles taux de parasitisme. Les espèces fortement parasitées se montraient moins agressives envers les vachers qu'envers d'autres espèces. Les individus agressifs présentaient également des taux de parasitisme inférieurs à ceux des individus moins agressifs vis-à-vis des intrusions dans leur territoire de nidification. Les individus appartenant à des espèces coloniales et nichant à l'intérieur des colonies étaient moins touchés par le parasitisme que les oiseaux nichant en dehors de la zone défendue par des voisins. Ainsi, les espèces non-agressives bénéficiaient d'une certaine protection contre le parasitisme du Vacher grâce à la défense territoriale plus vigoureuse des espèces voisines. Les données présentées ici sont parmi les premières recueillies à Porto Rico sur les interactions Vacher luisant / hôte parasité et, à ce titre, peuvent servir de repères pour mesurer des changements du comportement et de l'écologie au fil du temps.

Mots clés : agression, Antilles, défenses antiparasites, défense du nid hôte, défense du territoire, *Molothrus bonariensis*, parasitisme de couvée, rejet d'œuf, sélection de l'habitat, surveillance du nid, Vacher luisant

Most research on avian brood parasitism has been conducted in areas where the parasites have long coexisted with host populations. During this coexistence, parasites and host populations have coevolved strategies of exploitation and avoidance, some of which are now specialized enough to obscure their origin or possible evolutionary route. Study of the parasitic Shiny Cowbird (*Molothrus bonariensis*) and its host populations in the West Indies offers an opportunity to examine the biology of brood parasitism early in the history of interaction between a generalist parasite and a naïve local avifauna.

Shiny Cowbird has expanded its range northward recently from its native South America and Trinidad & Tobago through the West Indies and southeastern United States in response to favorable environmental changes resulting from man's conversion of forests to grazing and agricultural lands (Post and Wiley 1977a, Cruz *et al*. 1985, Post *et al.* 1993). This situation is comparable to the Brown-headed Cowbird's (*M. ater*) earlier range expansion in North America as original forests were converted to more favorable open habitat, and host populations naïve to social nest parasitism were exploited by the brood parasite (Mayfield 1965).

Shiny Cowbird arrived in Puerto Rico in the late 1940s or early 1950s (Post and Wiley 1977a). Because the local avian populations had no previous exposure to brood parasitism, I predicted that some populations would be vulnerable as cowbird hosts because they lacked effective anti-parasite strategies. Indeed, in the 1970s and 1980s, all nests examined of some species were parasitized, although none of the nests of other species were affected (Wiley 1985, Pérez-Rivera 1986).

Here, I present data on behavioral and ecological mechanisms that certain avian species in Puerto Rico use to avoid cowbird parasitism. These data were collected during the early period of Shiny Cowbird exploitation of Puerto Rican bird populations. My major thesis is that, though naïve through having no prior contact with brood parasitism, some species in the community may be preadapted to counter cowbird parasitism of their nests. These preadaptations may include surreptitious nest site selection and nest concealment; i.e., cryptic nests are more difficult for cowbirds to locate than nests in exposed sites. Therefore, habitat features that conceal host nests should be selected. I present a description of nesting habitat used by two Shiny Cowbird host species, Yellow Warbler (*Setophaga* *petechia*) and Yellow-shouldered Blackbird (*Agelaius xanthomus*). Some individuals may avoid parasitism by choosing certain components of their habitat that help to conceal their nests from prospecting cowbirds. I compare these components with those important in evading nest depredation to determine if some anti-predator defenses might serve as preadaptations to counter parasitism.

Some nesting birds will incubate parasitic eggs along with their own, others reject the parasitic eggs along with their own, and still others reject the parasite egg by building a new nest over the entire clutch, by abandoning and renesting at a different site, or by removing the parasitic egg from the nest. Parasite egg rejection is a host strategy selected as a defense against parasitism. Because Puerto Rican birds have only recently been exposed to cowbird parasitism, I predicted that rejection responses to parasitism would be rare.

Finally, I suggest that certain defense behaviors important in preventing nest depredation or in guarding one's territory against conspecifics or other competitors may be applicable to host-parasite confrontations. I expected that species that display high nest attendance, that are highly aggressive toward territory invaders, or both, would have a low incidence of cowbird parasitism. Species (or individuals) that spend a large proportion of the day near their nests during the critical pre-egglaying and laying periods are more likely to detect parasitism attempts and should be better able to thwart parasitism than those species with low nest attentiveness.

I expected that the recently arrived Shiny Cowbird would not be recognized as a potential threat by nesting species in Puerto Rico and would be attacked with less intensity than recognized competitors or nest predators. However, populations experiencing high parasitism rates (regardless of the recency of contact with the parasite) would be under severe selective pressure to develop discriminatory behavior and counter attempts of cowbirds to gain access to nests. Thus, birds experiencing the highest parasitism rates should have better-developed discriminatory and aggressive responses to cowbirds.

Aggressive individuals may be able to repel certain nest predators (Bump 1986, Knight and Temple 1988, Olendorf and Robinson 2000, Morrison *et al.* 2006). This aggression may also serve as a means of thwarting nest parasitism (Davies and Brooke 1988, Moksnes and Roskaft 1989, Neudorf and Sealy 1992, Uyehara and Narins 1995). I predicted that aggressive individuals would have lower rates of parasitism than individuals displaying low aggression toward predators and cowbirds.

STUDY AREAS

I studied brood parasitism at Roosevelt Roads Naval Station in easternmost Puerto Rico, and at Boquerón Forest, between Bahía Sucía and Bahía Montalva, in southwestern Puerto Rico. Both study areas are within the Subtropical Dry Forest Zone (Ewel and Whitmore 1973), although annual precipitation at Boquerón Forest ($\bar{x}$ = 74.4 cm) is about half that at Roosevelt Roads ($\bar{x}$ = 132.3 cm, 1959–2008; Southeast Regional Climate Center 2010). Most rainfall occurs in two periods in both study areas: May, and August through November. Buell and Dansereau (1966), Wiley (1985), Wiley and Wiley (1979), Wiley *et al.* (1991), and García *et al.* (1998) described these areas in greater detail.

Mangrove forest dominates the extensive tidal lands of both study areas. The forest at Roosevelt Roads is composed of four mangrove species: black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), button mangrove (*Conocarpus erectus*), and red mangrove (*Rhizophora mangle*). *Rhizophora* is nearest the sea and *Laguncularia* and *Conocarpus* are farthest inland. Australian beefwood (*Casuarina equisetifolia*), sweet acacia (*Vachellia farnesiana*), and leadtree (*Leucaena leucocephala*) occur in drier inland areas. Boquerón Forest consists of a red mangrove fringe (approximately 25% of the area), black mangrove forest (about 55%), and salt flats (10%) (Puerto Rico Department of Natural Resources 1976). A saltwort-(*Batis maritima*) *Avicennia* scrub and a mat of glasswort (*Salicornia*) or sea-purslane (*Sesuvium portulacastrum*) often characterize the sandy soils of the inner mangrove areas.

I conducted the research within mangrove forests because I wanted to restrict my work to a vegetatively simple ecosystem. This also made findings between my two study sites in southwestern and eastern Puerto Rico more comparable, as the two forests have the same dominant tree species, although structure differs somewhat.

METHODS

I collected data from 1975 to 1981, concentrating on three nesting species: Yellow-shouldered Blackbird, Yellow Warbler, and Greater Antillean Grackle (*Quiscalus niger*). Nests were located by thoroughly searching areas or watching for building activities from towers placed central to likely nesting habitat. Nest-centered 0.04-ha plots were used to sample habitat (James and Shugart 1970) after

Table 1. Description of quantitative habitat variables used in analysis of Yellow Warbler (*Setophaga petechia*) and Yellow-shouldered Blackbird (*Agelaius xanthomus*) nest site habitat, Puerto Rico.

Mnemonic	Description
TNUMBER	Number of trees (diameter > 7.6 cm) in the sample plot
TMEAN	Mean height (m) of trees in the sample plot
SNUMBER	Number of shrubs (diameter ≤ 7.6 cm) in the sample plot
SMEAN	Mean height (m) of shrubs in the sample plot
PGND	Percentage ground cover
PCAN	Percentage canopy cover
NHEIGHT	Height (cm) of nest tree
DBH	Diameter (cm) of nest tree at breast height
HNEST	Height (cm) of nest
DNEST	Distance (cm) of nest from tree center
VPLANE	Angle (degrees) of unobstructed vision from nest in vertical plane
HPLANE	Angle (degrees) of unobstructed vision from nest in horizontal plane
VDIST	Distance (m) of unobstructed vision from nest in vertical plane
HDIST	Distance (m) of unobstructed vision from nest in horizontal plane

chicks had fledged or once nests failed. Within the plots, I measured 14 habitat parameters selected for possible relevance to nest concealment (Table 1).

To determine host response to cowbird eggs, I observed the fate of alien eggs deposited in nests. Generally, species that reject cowbird eggs cannot be determined from observations of naturally occurring parasitism. Therefore, I followed Rothstein's (1971, 1975a, b) technique of artificial parasitism to detect which nesting species reject or accept alien eggs. I used both real and artificial cowbird eggs. Cowbird eggs were obtained from nests in other parts of the study area where experiments were not performed. Artificial cowbird eggs were constructed of lathe-shaped pine wood and coated with epoxy paint to simulate the color pattern of cowbird eggs. Size and weight of the artificial eggs closely approximated Shiny Cowbird eggs. I removed one host egg when the cowbird egg was added to the nest. Artificial parasitism was performed within the first two hours after dawn, the natural laying period of female Shiny Cowbirds (Hoy and Ottow 1964, J. W. Wiley pers. obs.). All rejection experiments were performed in an area adjacent to the main monitoring area for nesting birds. See Cruz *et al.* (1985, 1989) for further details on experiments.

Two mutually exclusive responses to parasite eggs are possible: acceptance or rejection. I have followed Rothstein's (1975a) terminology for hosts that reject cowbird eggs as "rejectors," and those that do not as "acceptors." Rejection usually occurs by ejection of the parasite egg, but I also scored desertion and nest build-overs as rejection. I used Rothstein's (1975a) criterion of 5 days for rejection.

Responses of residents to territory intruders were determined by watching nesting birds from blinds and towers. Towers (3.3–5 m tall) with observation blinds were positioned 2–4 m from, and on a level with or slightly above, nests. I used 10 × 40 binoculars and a 15–60× zoom spotting scope to make observations. Narrative notes were written or spoken into a portable tape recorder and transcribed later. I used data forms, on which host and cowbird activities had been categorized, to score behavior. Most nest searching and laying activity by cowbirds occurs in the early morning, so I concentrated my observations at nests from dawn through 1100. A total of 208 hr was spent observing nesting behavior from blinds.

I scored attentiveness at nests by noting time adults were (1) on the nest, (2) off the nest, but within 10 m of the nest, and (3) beyond 10 m from the nest. U. S. Fish and Wildlife Service numbered metal bands and unique combinations of colored celluloid leg bands were used to identify individual birds. I recorded the species of intruder and the resident's (male and female) reaction to the alien at eight predetermined, marked distances (0.0–0.4, 0.5–0.9, 1.0–1.9, 2.0–2.9, 3.0–4.9, 5.0–9.9, 10.0–19.9, ≥ 20 m). The overt responses of the residents were scored on data sheets in the following predetermined categories: 0 = resident shows no detectable reaction to alien's presence; 1 = resident orients toward intruder, gives low-intensity calls; 2 = resident leaves nest, moves in direction of intruder, gives alarm calls; 3 = resident flies at intruder, supplants, and chases it from territory; 4 = resident strikes intruder, grapples, and plucks intruder's feathers.

Botanical nomenclature follows Otero *et al.* (1945), Little and Wadsworth (1964), and Little *et*

Table 2. Tree and shrub species composition of 0.04 ha sample plots centered on Yellow Warbler (*Setophaga petechia*) and Yellow-shouldered Blackbird (*Agelaius xanthomus*) nests at Roosevelt Roads (RR) and Boquerón Forest (BF), Puerto Rico, 1975–1981.

			Frequency[a] (Number[b]) for Each Tree and Shrub Species[c] on Plot					
Bird species	Site	*n*	*Avicennia*	*Rhizophora*	*Laguncularia*	*Casuarina*	*Vachellia*	*Leucaena*
Yellow Warbler	RR	55	100.0 (83.1)	18.2 (6.5)	18.2 (7.1)	1.8 (<0.1)	1.8 (<0.1)	1.8 (1.8)
Yellow-shouldered Blackbird	RR	33	100.0 (100.0)					
Yellow-shouldered Blackbird	BF	28	96.4 (69.5)	53.6 (30.5)				

[a] Percent of plots containing the species.

[b] Numerical percentage composition in plot.

[c] *Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa*, *Casuarina equisetifolia*, *Vachellis farnesiana*, *Leucaena leucocephala*.

al. (1974). Bird names follow the American Ornithologists' Union (2012).

Statistical methods follow Zar (1974), Hollander and Wolfe (1973), Pielou (1977), and Kleinbaum and Kupper (1978). Discriminant analyses were performed using the Statistical Package for the Social Sciences (SPSS; Nie *et al.* 1975). When the underlying assumptions (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 to those samples. Significance level was set at 0.05. Standard errors are presented as the measure of variance about the mean.

RESULTS

NESTING HABITAT STRUCTURE AND COWBIRD AVOIDANCE

Nest habitat composition.—Black mangrove was the dominant vegetation in the habitat plots for nesting Yellow Warblers and Yellow-shouldered Blackbirds at Roosevelt Roads Naval Station and Boquerón Forest (Table 2). Whereas blackbird sample plots at Roosevelt Roads contained pure stands of black mangrove (all blackbird nests were in black mangrove), red mangrove occurred in 53.6% of the Boquerón plots and comprised 30.5% of the vegetation. In the southwestern (Boquerón) study area, 80% of Yellow-shouldered Blackbird nests ($n = 32$) were in black mangrove and 20% ($n = 8$) were in red mangrove, a proportion not different from expected based on the availability of the species (Kolmogorov-Smirnov test, $P > 0.05$).

Vegetation in Yellow Warbler nest plots at Roosevelt Roads was more diverse than in Yellow-shouldered Blackbird plots (Table 2), yet nearly all nests (96.5%; $n = 55$) were in black mangrove. Only one nest (1.8%) was found in red mangrove and one in white mangrove. Nevertheless, warbler use of nest vegetation did not differ from that expected based on species availability (Kolmogorov-Smirnov test, $P > 0$ .05).

Breeding warblers and blackbirds exhibited a broad use of vegetative components within habitat selected for nesting (i.e., range values in Table 3). Mean component values for nest habitat of Yellow Warblers were greater than those of Yellow-shouldered Blackbirds in SNUMBER, SMEAN, and PGND, whereas values for TNUMBER, PCAN, DBH, DNEST, and HDIST were greater for blackbirds than for warblers; i.e., warblers nested in denser shrub vegetation with more ground cover than blackbirds, which nested in areas with more and larger trees, with denser canopies, and with greater unobstructed vision in the horizontal plane (Table 3).

Habitat selection and parasite avoidance.—I conducted stepwise discriminant analyses based on certain linear combinations of the predictor variables on blackbird and warbler nest sites to establish optimal "separation" of the groups "Parasitized" and "Non-parasitized," with the null hypothesis of no between-group difference in the variable selected. One objective of the analysis was to predict the category to which an observation belonged; i.e., whether a nest belonged to the parasitized or non-parasitized category based on the predictive habitat

Table 3. Sample means, standard errors, and ranges of habitat variables for parasitized and non-parasitized Yellow Warbler (*Setophaga petechia*) and Yellow-shouldered Blackbird (*Agelaius xanthomus*) nest sites at Roosevelt Roads, Puerto Rico, 1975–1981. Only variables that were used in analyses are listed. Range of measurements is given in parentheses under mean and standard error. Sample sizes are given in parentheses in column headings. Variable descriptions are presented in Table 1.

	Yellow Warbler			Yellow-shouldered Blackbird		
Variable	Unparasitized (10)	Parasitized (35)	Total (45)	Unparasitized (3)	Parasitized (55)	Total (58)
TNUMBER	52.7 ± 19.3 (0–201)	30.7 ± 4.8 (0–143)	35.6 ± 5.7 (0–201)	57.0 ± 11.6 (34–71)	56.9 ± 8.5 (0–292)	56.9 ± 8.0 (0–292)
TMEAN (m)	2.2 ± 0.3 (1.2–7.6)	2.8 ± 0.2 (1.4–7.6)	2.7 ± 0.1 (1.2–7.6)	2.2 ± 0.3 (1.2–7.3)	3.7 ± 0.3 (1.2–11.6)	3.6 ± 0.3 (1.2–11.6)
SNUMBER	132.1 ± 29.3 (15–224)	201.5 ± 38.5 (2–1520)	186.1 ± 30.8 (2–1520)	21.7 ± 13.3 (5–48)	76.9 ± 28.6 (0–932)	74.1 ± 27.1 (0–932)
SMEAN (m)	1.1 ± 0.1 (0.1–2.1)	1.0 ± 0.1 (0.1–2.1)	1.0 ± 0.04 (0.1–2.1)	0.7 ± 0.1 (0.2–1.1)	0.8 ± 0.1 (0.2–2.0)	0.8 ± 0.1 (0.2–2.0)
PGND	19.0 ± 4.8 (0–40)	19.8 ± 4.0 (3–100)	19.6 ± 2.3 (0–100)	0.0	3.7 ± 1.3 (0–80)	3.6 ± 1.2 (0–80)
PCAN	9.9 ± 3.0 (0–30)	11.5 ± 2.2 (0–40)	11.2 ± 1.9 (0–40)	10.0 ± 5.0 (5–20)	17.0 ± 1.2 (0–88)	16.7 ± 2.3 (0–88)
NHEIGHT (cm)	209.8 ± 12.9 (145–274)	213.6 ± 14.4 (58–549)	212.8 ± 11.5 (58–549)	189.0 ± 49.7 (102–274)	350.3 ± 27.7 (25–975)	342.0 ± 26.8 (25–975)
DBH (cm)	2.1 ± 0.4 (0.8–4.3)	2.1 ± 0.3 (0.4–8.5)	2.2 ± 0.2 (0.4–8.5)	4.6 ± 0.3 (4.0–4.9)	3.3 ± 0.3 (0.6–19.4)	3.4 ± 0.3 (0.6–19.4)
HNEST (cm)	117.4 ± 8.6 (76–168)	104.9 ± 7.2 (18–193)	107.7 ± 5.9 (18–193)	100.7 ± 23.0 (58–137)	184.5 ± 13.2 (14–488)	180.1 ± 12.8 (14–488)
DNEST (cm)	39.0 ± 14.1 (0–125)	40.5 ± 9.7 (0–227)	40.1 ± 8.1 (0–227)	131.3 ± 63.5 (5–205)	60.9 ± 11.1 (0–305)	64.6 ± 11.0 (0–305)
VPLANE (°)	30.0 ± 11.1 (0–90)	28.4 ± 5.5 (0–90)	28.8 ± 4.9 (0–90)	56.7 ± 51.7 (10–160)	24.7 ± 6.9 (0–180)	26.4 ± 6.9 (0–180)
HPLANE (°)	39.0 ± 12.2 (0–120)	35.6 ± 7.0 (0–140)	36.3 ± 6.0 (0–140)	0.0	48.2 ± 12.2 (0–360)	45.7 ± 11.7 (0–360)
HDIST (m)	13.8 ± 5.5 (5–91)	13.6 ± 2.9 (5–61)	13.7 ± 2.5 (5–91)	40.7 ± 40.6 (8–85)	95.9 ± 47.2 (0–1524)	93.1 ± 44.8 (0–1524)
VDIST (m)	20.5 ± 8.5 (4–61)	15.6 ± 3.6 (5–61)	16.7 ± 3.3 (4–61)	2.7 ± 2.7 (0–122)	91.9 ± 47.9 (0–1500)	87.3 ± 45.5 (0–1500)

variates. The other objective was to provide insight, through differential patterns of habitat use by individuals, into why some nests were parasitized and others were not.

From the univariate *F*-ratio (1, 43), TMEAN was determined to be the best of the 14 variables examined in discriminating between parasitized and non-parasitized nests of Yellow Warblers ($F_{\text{TMEAN}} = 3.52$), although none of the variables showed significant discriminatory ability (all $P > 0.05$). Next, I used a stepwise procedure to select the single best discriminatory variable. Prior probabilities for Group 1 (Non-parasitized) and Group 2 (Parasitized) were 0.22 and 0.78, respectively. As predicted by the univariate *F*-ratio, the variable TMEAN was entered on step one and had the highest value on the selection criterion. In step two, the variable TNUMBER was selected as best among the remaining variables to be able to improve the value of the discrimination criterion in combination with TMEAN. In step three, the variable NHEIGHT was added. The remaining variables did not contribute to further discrimination of the groups. Thus, the stepwise discriminant analysis of nesting habitat versus brood parasitism for Yellow Warbler nests ($n = 45$) produced one discriminant function (TMEAN + TNUMBER + NHEIGHT) that accounted for all the among-group variability. Wilks' lambda (λ) values decreased with the addition of variables (TMEAN = 0.92, TMEAN + TNUMBER = 0.83), and TMEAN + TNUMBER + THEIGHT = 0.79), indicating an improvement in discrimination ability of the function ($\chi^2 = 9.7$, df = 3, $P < 0.03$).

The overall correct classification of membership in Group 1 (non-parasitized) and Group 2 (parasitized) nest sites was high (84.4%) for Yellow Warblers. The apparent error rates were 60% (n_{12} / n_1) and 2.9% (n_{21} / n_2). Calculation of estimated error rates showed good probability of correctly classifying parasitized nests ($P_2 < 0.05$), but poor probability of correctly classifying non-parasitized nests ($P_1 > 0.05$).

The univariate *F*-ratio (1, 56) for Yellow-shouldered Blackbird habitat showed HNEST to be the best of the 14 variables in discriminating between parasitized and non-parasitized nest sites ($F_{\text{HNEST}} = 2.15$) although, as with the other variables examined, HNEST did not show significant discriminatory ability ($P > 0.05$). In the stepwise procedure for selecting the single best discriminatory variable, prior probabilities for Group 1 (Non-parasitized) and Group 2 (Parasitized) were 0.05 and 0.95, respectively. The variable HNEST was entered on step one. In step two, the variable DNEST was selected as the best among the remaining variables to improve the values of the discrimination criterion in combination with HNEST. None of the other variables contributed to further discrimination of the group at the minimum level I set to enter the stepwise analysis. Wilks' lambda value for HNEST was 0.96, and 0.94 for the combined effects of HNEST and DNEST. The addition of DNEST decreased the lambda, indicating an improvement in discrimination ability ($\chi^2 = 3.5$, df = 2, $P > 0.05$). Thus, non-parasitized blackbird nests were placed lower and farther from the tree center than parasitized nests.

The correct classification of membership of Yellow-shouldered Blackbird nests in Group 1 (non-parasitized) and Group 2 (parasitized) was high (94.8%), with both groups having 100% predicted group membership.

Another approach to analysis of host nesting habitat selection relative to rate of parasitism is to compare the number of cowbird eggs laid per nest with habitat variables that would make the nest less obvious to brood parasites. Yellow-shouldered Blackbirds showed significant correlation (Pearson product moment, $P < 0.05$) with only one habitat variable, SNUMBER; i.e., blackbird nests situated in denser shrub areas had fewer cowbirds eggs. ANOVA testing revealed that only HNEST was significant relative to number of cowbird eggs laid in Yellow Warbler nests; i.e., lower-placed warbler nests had fewer cowbird eggs.

Habitat structure and nest depredation.— Selection of certain habitat components important in concealing nests from predators may also have value in camouflaging nests from brood parasites. Nesting species in Puerto Rico have been exposed to nest predators far longer than to brood parasites. Thus, those habitat parameters useful in thwarting nest-locating attempts of cowbirds may have been selected first as anti-depredation strategies. To explore this possibility, I compared success (FATE) of Yellow Warbler and Yellow-shouldered Blackbird nests with nesting habitat structure. I predicted that individuals using habitats that enhanced nest concealment would exhibit improved nest success over individuals with more exposed nests. Only nests that were successful or that failed because of depredation were used in the analysis; deserted nests were not included.

ANOVA testing of Yellow Warbler habitat revealed that the variables SMEAN ($F = 5.22$, $P < 0.03$) and VDIST ($F = 5.11$, $P < 0.05$) were significant in discriminating between successful and unsuccessful nests. Univariate *F*-ratio for Yellow-shouldered Blackbird nest habitat failed to yield important variables for discrimination.

I used discriminant analysis to determine habitat correlates with nest success of warblers and blackbirds. For the warbler, SMEAN ($\lambda = 0.8918$) was followed in sequence of importance by NHEIGHT ($\lambda = 0.8210$), TMEAN ($\lambda = 0.74$), and PCAN ($\lambda = 0.71$). The chi-square statistic ($\chi^2 = 17.0$, df = 6, $P < 0.01$) associated with the single discriminant function revealed that function was significant in distinguishing between successful and unsuccessful nesting efforts. These four variables indicated that suc-

Table 4. Responses of 14 species of nesting birds to experimental parasitism at nests, Roosevelt Roads Naval Station and Boquerón Forest, Puerto Rico, 1977–1981. Real or artificial cowbird eggs were placed in potential host nests within the first two hours after dawn. See text for details of experimental design.

Species	No. of Nests	Egg Rejection	Egg Acceptance	% Eggs Rejected	% Nests Parasitized
Puerto Rican Flycatcher (*Myiarchus antillarum*)	7	0	7	0	85
Yellow Warbler (*Setophaga petechia*)	17	0	17	0	76
Puerto Rican Oriole (*Icterus portoricensis*)	7	0	7	0	100
Nutmeg Mannikin (*Lonchura punctulata*)	15	0	15	0	0
Black-faced Grassquit (*Tiaris bicolor*)	6	0	6	0	0
Yellow-shouldered Blackbird (*Agelaius xanthomus*)	11	1	10	9.1	93
Greater Antillean Grackle (*Quiscalus niger*)	36	32	4	11.1	11
Black-whiskered Vireo (*Vireo altiloquus*)	3	1	2	33.3	82
Bananaquit (*Coereba flaveola*)	13	9[a]	4	69.2	0
Northern Mockingbird (*Mimus polyglottos*)	7	5	2	71.4	2
Pearly-eyed Thrasher (*Margarops fuscatus*)	21	17	4	81.0	0
Gray Kingbird (*Tyrannus dominicensis*)	18	15	3	83.3	1
Red-legged Thrush (*Turdus plumbeus*)	3	3	0	100	4
Puerto Rican Spindalis (*Spindalis portoricensis*)	2	2	0	100	0

[a] Desertions.

cessful Yellow Warbler nests were in stands composed of shorter trees or taller shrubs, or both, in sites with greater canopy cover, and were placed lower in the vegetation than unsuccessful nests. Prediction results for the classification of memberships in Group 1 (Unsuccessful) and Group 2 (Successful) showed the overall correct classification of warbler nest sites was high (86.7%), with correct predicted group membership rates of 90.3% (n_{12} / n_1) and 78.6% (n_{21} / n_2), respectively.

As predicted from the univariate F-ratio ($F = 2.38$, $P < 0.05$), the discriminant analysis of Yellow-shouldered Blackbird nest habitat entered VDIST ($\lambda = 0.96$) at step one; i.e., successful nests had greater visual distance than unsuccessful nests. No other variables were entered. The discriminant function did not significantly explain fate of blackbird nests ($\chi^2 = 2.3$, df = 1, $P > 0.05$). The percent of "grouped" cases correctly classified for blackbirds was 66.7%, with correct predicted group membership of 97.3% in Group 1 (unsuccessful) and 100% in Group 2 (successful) nests.

Host discrimination.—Contrary to the prediction that rejection behavior would be rare in Puerto Rico because of the recent exposure of native bird populations to brood parasitism, several species did reject eggs from artificially parasitized nests (Table 4). The response distribution was bimodal, with a peak at 0% rejection and a smaller, less defined peak between 80% and 100%. To test whether the bimodality was significant, the abscissa was divided into three equal (33.3%) regions. The distribution departed from uniform expectations for each region ($G = 11.62$, $\chi^2_{0.005(2)} = 10.60$).

Regularly parasitized species (≥ 69% of nests parasitized) showed no or only occasional egg rejection. Rarely parasitized species (< 4% of nests parasitized) usually rejected alien eggs. Grackles, which were parasitized at an intermediate rate (11%), accepted most cowbird eggs placed in their nests.

I found no association between percent rejection and incidence of parasitism in the eight acceptor species ($r = -0.20$; $P > 0.05$). Similarly, no association between percent rejection and parasitism rate in the rejector species was evident ($r = -0.34$, $P > 0.05$). There was no association between percent rejection and the probable reproductive losses caused by Shiny Cowbird ($r^2_{\text{nest success}} = 0.24$, $r^2_{\text{clutch size}} = 0.03$, $r^2_{\text{no. fledged}} = 0.03$; all $P > 0.05$, t-test).

I found low rates of egg burial by hosts at nests of parasitized Yellow Warblers and Yellow-shouldered Blackbirds: 3.1% (5 of 160; all Roosevelt Roads) of the warbler nests and 2.4% (5 of 206; 3 of 128 at Roosevelt Roads and 2 of 78 at Boquerón Forest) of the blackbird nests (Fig. 1). All observed cases of egg burial were at nests where the cowbird laid its egg(s) before the host laid its eggs. Three of the built-over nests (30%) subsequently had host eggs laid in the newly lined nests. Each of those

Fig. 1. Yellow Warbler (*Setophaga petechia*) nest showing build-over of original level of nest (at position of pen) after Shiny Cowbird (*Molothrus bonariensis*) laid an egg in nest with one warbler egg (at end of pen: warbler egg on left and cowbird egg on right).

nests was again parasitized, and the hosts incubated the eggs.

Host nest attentiveness.—I found a negative relationship between species' nest attentiveness and level of parasitism during the pre-egglaying and laying stages at Roosevelt Roads (r = -0.95, P = 0.05; t-test). Gray Kingbirds (*Tyrannus dominicensis*) were the most attentive of four species watched during pre-egglaying and early egglaying (Table 5). Although adult kingbirds were off the nest much of the day, the proportion of the time they spent nearby (within 10 m, hence presumably able to detect cowbirds near their nest and defend against cowbird entry into their nest) was high. Pre-egglaying and laying female kingbirds were consistently within sight of their nests during all my observations. Male kingbirds also showed high nest attendance; they were within 10 m their nest for more than 50% of my observation time (n = 26.7 hr).

Greater Antillean Grackles also showed high attendance during the pre- and early egglaying period, with one or both pair members in nest areas 93% of the observation time (n = 1.2 hr; Table 5). In contrast to the kingbird attendance pattern, however, female grackles regularly left the area to forage with males.

Yellow Warbler and Yellow-shouldered Blackbird attendance rates during the pre-egglaying and laying periods were much lower than those of kingbirds and grackles (Table 5). Nests were left unguarded for up to 86% of the total observation time (n = 16.3 hr for warblers, 10.1 hr for blackbirds), which allowed prospecting cowbirds easy access (Fig. 2B–E). Blackbirds and warblers incurred the highest rates of parasitism among the four species. The pattern of nest attentiveness was similar among the four species, with high attentive rates during late incubation (range = 71.0–89.5%) and much lower rates during the nestling period (13.2–32.6%; Gray Kingbird not watched) (Table 5).

Host aggressiveness.—Rate of parasitism was negatively correlated with a species' aggressive response toward Shiny Cowbird (r = -0.94, $r_{0.05(2),6}$ = 0.71, $P < 0.001$); i.e., aggressive species were parasitized less often than species showing low aggressive responses. Aggressive responses among only acceptor species (n = 4) showed a lower association with parasitism rates (r = -0.83, $r_{0.05(2),2}$ = 0.95, $P > 0.05$) than did responses among rejector species (n = 4; r = -0.14, $P > 0.05$).

I compared responses of nesting species to cowbird presence with their responses to other (non-cowbird) species to determine if differences existed in host discrimination among species. Responses to cowbirds by parasitized and non-parasitized species were also compared to determine if regularly parasitized birds displayed higher aggression toward cowbirds than non-parasitized species.

I found differences in responses to intruders (cowbird and other species entering the resident's nesting area) among the eight species watched ($P < 0.001$, Friedman 2-way ANOVA; Table 6). Regularly parasitized species displayed lower aggressive responses to cowbirds than did non-parasitized species (P = 0.05; Fig. 3A). Host response to Shiny Cowbirds differed significantly among the parasitized species ($P < 0.05$), with Yellow Warblers displaying the lowest aggression toward cowbird intruders (Table 6). Warbler aggression was significantly less than that of Yellow-shouldered Blackbirds ($P < 0.02$), but there were no other differences among the three parasitized species. The five non-parasitized species did not differ in their aggressive response to Shiny Cowbird ($P > 0.05$; Table 6).

Intensity of aggression toward non-cowbird intruders varied among the eight observed species ($P < 0.001$, Friedman 2-way ANOVA; Table 6). Puerto Rican Orioles (*Icterus portoricensis*) displayed lower intensity responses ($P < 0.05$) than other species, whereas Puerto Rican Spindalis

Table 5. Nest attendance behavior of four passerine bird species during four breeding season stages, Roosevelt Roads Naval Station, eastern Puerto Rico, 1978–1981.

Period and Species	Observation Time (hr)	Number of Nests	Time (min) Adult on Nest		Time (min) Adult off Nest		% Time Adult off Nest but < 10 m
			%	$\bar{x}$ ± SE	%	$\bar{x}$ ± SE	
Nest building							
Yellow-shouldered Blackbird	15.4	5	18.6	2.0 ± 1.2	81.4	14.8 ± 12.7	6.7
Greater Antillean Grackle	4.9	2	51.4	4.7 ± 3.8	48.6	3.4 ± 0.8	1.0
Yellow Warbler	2.7	2	4.4	1.0 ± 0.8	95.7	19.5 ± 2.7	–
Gray Kingbird ♀	1.6	1	0	–	100.0	95.0 ± 0.0	100.0
Gray Kingbird ♂	1.6	1	9.0	1.7 ± 1.4	91.1	14.4 ± 10.0	76.0
Pre-egglaying and early egglaying							
Yellow-shouldered Blackbird	10.1	2	16.2	4.0 ± 2.7	83.8	16.9 ± 2.5	–
Greater Antillean Grackle	1.2	1	93.1	16.8 ± 12.0	6.9	2.5 ± 2.1	–
Yellow Warbler	16.3	6	13.4	2.1 ± 1.9	86.4	13.1 ± 10.1	–
Gray Kingbird ♀	4.1	2	13.7	2.6 ± 1.3	86.3	15.0 ± 0.9	86.3
Gray Kingbird ♂	4.1	2	–	0	100.0	245.0 ± 0.0	51.7
Incubation							
Yellow-shouldered Blackbird	38.6	9	75.6	29.6 ± 26.1	24.5	8.8 ± 3.3	9.6
Greater Antillean Grackle	18.6	16	71.4	14.6 ± 7.6	28.6	4.4 ± 2.4	–
Yellow Warbler	23.0	6	81.3	9.1 ± 5.9	18.7	3.1 ± 2.9	–
Gray Kingbird ♀	21.0	11	89.5	68.0 ± 54.3	8.2	4.5 ± 4.0	0
Gray Kingbird ♂	14.9	7	40.5	60.3 ± 77.0	59.5	53.4 ± 21.0	0
Young chicks							
Yellow-shouldered Blackbird	25.5	8	32.6	4.2 ± 2.9	67.4	7.9 ± 4.2	4.2
Greater Antillean Grackle	4.1	4	26.7	4.7 ± 4.6	73.3	7.2 ± 2.1	–
Yellow Warbler ♀	4.3	5	13.2	0.5 ± 0.2	86.8	3.1 ± 1.2	–
Yellow Warbler ♂	4.3	5	7.5	0.6 ± 0.3	92.5	6.1 ± 3.7	–

(*Spindalis portoricensis*) and Northern Mockingbirds (*Mimus polyglottos*) were more aggressive toward non-cowbirds than were other species ($P < 0.005$). Gray Kingbirds, Red-legged Thrushes (*Turdus plumbeus*), Yellow-shouldered Blackbirds, Yellow Warblers, and Greater Antillean Grackles showed similar responses toward non-cowbird aliens ($P > 0.05$). Non-parasitized species were consistently more aggressive toward non-cowbird species than were parasitized species ($P < 0.01$, Friedman 2-way ANOVA; Fig. 3B).

Several species displayed different responses to cowbirds compared to other species of intruders (Table 7). Whereas tanagers and mockingbirds exhibited no difference in response to cowbirds compared with non-cowbird intruders, kingbirds, grackles, and thrushes displayed greater aggression toward the parasites than toward other species in the middle distance from nests, and grackles also showed greater aggressive behavior in the closest distance interval.

Regularly parasitized species also showed differences between their responses to cowbirds and non-cowbirds at their nests (Table 7). Yellow-shouldered Blackbirds displayed less aggression toward cowbirds than toward other species at mid-ranges (significantly different overall, $P < 0.02$, Friedman 2-way ANOVA), whereas orioles exhibited greater hostility toward cowbirds at mid-ranges. Yellow Warblers were less aggressive to cowbirds than to other intruders in all distance intervals sampled ($P < 0.02$).

I observed individual differences in intensity of aggression toward nest intruders. Aggressive responses of 45 nesting female Yellow Warblers were compared with the number of cowbird eggs laid in their nests. The number of cowbird eggs laid in a host's nest is a realistic indicator of how successful

Fig. 2. Shiny Cowbird (*Molothrus bonariensis*) and host behavior in Puerto Rico. A. Female cowbird on elevated perch watching potential host activities. B and C. Female cowbird approaching and inspecting nest after female and male Yellow Warblers (*Setophaga petechia*) had left nest area. D. Female cowbird inspecting contents of Yellow Warbler nest, which contained one recently laid warbler egg. Cowbird punctured the warbler egg, but left it in place. E. Female cowbird laying egg in Yellow-shouldered Blackbird (*Agelaius xanthomus*) nest when hosts were away from nest area. F. Female cowbird, in the process of laying egg, attacked by returning adult male and female Yellow-shouldered Blackbirds. Blackbirds are pecking and tugging on head feathers of cowbird, but parasite remained on nest until her egg was laid.

Table 6. Mean values for aggressive responses[a] to intruder of eight nesting bird species toward Shiny Cowbird (*Molothrus bonariensis*) and non-cowbird intruders at eight distance intervals from their nests, Roosevelt Roads Naval Station, Puerto Rico, 1978–1981.

	Distance from Resident's Nest (m)							
Species[b] and Interaction Component	0.0–0.4	0.5–0.9	1.0–1.9	2.0–2.9	3.0–4.9	5.0–9.9	10.0–19.9	≥ 20
Regularly parasitized species								
Yellow-shouldered Blackbird								
with all species	2.9	2.9	2.5	2.3	1.9	0.9	0.7	0.1
with non-cowbird	3.3	3.2	2.7	2.7	2.2	1.0	0.8	0.1
with only cowbird	2.5	2.1	1.9	1.4	1.3	1.0	0.1	0.0
Puerto Rican Oriole								
with all species	1.9	1.5	1.1	0.8	0.8	0.1	0.1	0.1
with non-cowbird	2.1	1.4	1.0	0.5	0.8	0.0	0.1	0.1
with only cowbird	2.1	1.6	1.3	1.2	0.9	0.0	0.0	0.0
Yellow Warbler								
with all species	2.0	2.5	2.2	2.0	1.6	1.3	0.5	0.0
with non-cowbird	2.8	2.8	2.8	2.2	1.9	1.6	0.6	0.0
with only cowbird	1.4	1.7	0.4	0.4	0.4	0.6	0.0	0.0
Non-parasitized or irregularly parasitized species								
Gray Kingbird								
with all species	2.9	3.0	2.5	2.3	2.4	1.9	1.0	0.6
with non-cowbird	2.9	3.0	2.5	2.2	2.4	1.8	1.0	0.7
with only cowbird	3.5	2.8	2.9	2.8	2.4	3.2	0.6	0.4
Puerto Rican Spindalis								
with all species	3.8	3.1	3.0	3.0	2.9	2.3	2.7	2.4
with non-cowbird	3.4	3.2	3.0	3.0	2.8	2.8	2.7	2.4
with only cowbird	3.9	3.1	3.0	3.0	3.0	2.3	–	–
Greater Antillean Grackle								
with all species	3.1	2.8	2.5	1.9	1.9	1.2	1.0	0.4
with non-cowbird	2.9	2.7	2.4	2.6	1.7	0.9	1.0	0.6
with only cowbird	3.4	3.2	2.9	2.3	2.4	2.0	1.0	0.0
Red-legged Thrush								
with all species	3.3	3.1	2.9	2.7	2.1	1.8	0.9	0.6
with non-cowbird	3.4	3.1	2.8	2.6	1.8	1.0	0.2	0.0
with only cowbird	3.2	3.0	3.0	3.0	3.0	3.0	1.6	0.1
Northern Mockingbird								
with all species	3.3	3.4	3.2	3.0	3.0	2.9	2.7	1.4
with non-cowbird	3.4	3.4	3.2	3.2	3.2	2.8	2.8	1.6
with only cowbird	3.2	3.3	3.2	2.8	2.9	3.0	2.4	1.0
Means for all nesting species	2.8	2.6	2.3	2.1	2.0	1.4	0.8	0.4

[a] Aggressive index of resident's behavior toward intruder: 0 = no reaction by resident to alien's presence; 1 = resident turns on nest to orient toward intruder; 2 = leaves nest, moves in direction of intruder, gives alarm calls; 3 = flies at intruder, supplants, and chases alien; 4 = strikes intruder, grapples, plucks intruder's feathers.

[b] See Table 4 for scientific names.

an individual is at repelling a brood parasite. Several female cowbirds may be involved in laying eggs in a host's nest; I observed up to four cowbirds (uniquely color banded) laying eggs in one Yellow Warbler nest. Multiple parasitism reflects the minimum number of times cowbirds were able to penetrate a host's defenses. The mean aggressive index of parasitized female warblers (0.8) was significantly lower than that of non-parasitized female warblers (2.7; $P < 0.001$, median test). Further, the average aggressive index of successful warbler individuals was higher than for unsuccessful nesters (1.6 vs. 1.0), although the difference was not statistically significant ($P > 0.05$).

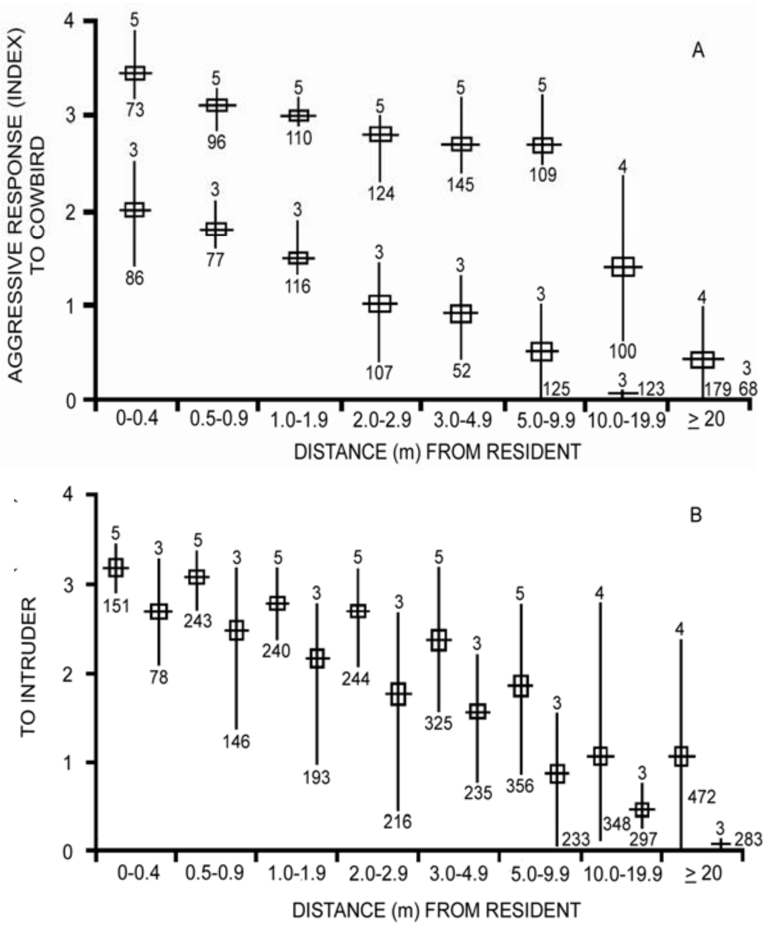

Fig. 3. Mean aggressive responses of breeding bird species toward avian intruders approaching nest sites. Horizontal line represents the mean, vertical line the range, and box one standard error about the mean. The number of nesting species in each category is presented above the range line. The number of encounters observed is presented below or to the right of the range line. Aggressive response index is described in Table 6 (0 = least aggressive, 4 = most aggressive response). Names of species observed are presented in Table 4. (A) Mean aggressive responses of parasitized (lower figures for each distance interval) and non-parasitized (upper figures) species toward Shiny Cowbirds (*Molothrus bonariensis*) at eight distance intervals from the nesting birds. None of the three parasitized species demonstrated aggressive behavior toward cowbirds beyond 20 m. (B) Mean aggressive responses of parasitized (right figures of pairs for each distance interval) and non-parasitized (left figures of pairs) species toward intruding species other than Shiny Cowbird at eight distance intervals from the resting birds.

Colonial nesting and brood parasitism.—Greater Antillean Grackles typically nested in loose colonies and defended areas with a radius of 10–20 m (Table 6) in the Roosevelt Roads study area. I found that parasitized grackle nests were farther from other active grackle nests than were non-parasitized nests (mean inter-nest distance for parasitized nests = 35.3 ± 10.9 m; mean for non-parasitized nests = 9.7 ± 1.9 m; $P < 0.05$, Mann-Whitney 2-sample test). Location of a grackle nest in the breeding area was important to whether it was parasitized by cowbirds. Parasitized nests ($n = 13$) were more often located along the colony edge (more than 8 m from active nests; $n = 5$) or were solitary (more than 20 m from other nests; $n = 7$); only one nest was parasitized within the core of an active colony. Non-parasitized nests included 49 in the core or within 8 m of an active grackle nest in the colony, one at the

Table 7. Aggressive responses (defined in Table 6) of nesting passerines to presence of Shiny Cowbird (*Molothrus bonariensis*) and non-cowbird intruder in nest areas at Roosevelt Roads Naval Station, Puerto Rico. H_o: Response of nesting bird to cowbird = response to non-cowbird.

		Distance from Nesting Bird (m)							
Nesting Species[b]	Statistic	0–0.4	0.5–0.9	1.0–1.9	2.0–2.9	3.0–4.9	5.0–9.9	10.0–19.9	≥ 20
Yellow-shouldered Blackbird	Dmax	0.32	0.33	0.28	0.49	0.43	0.18	0.31	0.09
	Significance	0.09	0.21	0.10	0.001[a]	0.03[a]	0.49	0.16	1.20
Puerto Rican Oriole	Dmax	0.14	0.19	0.23	0.31	0.74	0.03	0.16	0.19
	Significance	1.42	0.36	0.09	0.003[a]	1.77	1.90	0.28	0.31
Yellow Warbler	Dmax	0.58	0.63	0.59	0.65	0.56	0.49	0.25	–
	Significance	>0.0001[a]	>0.0001[a]	>0.0001[a]	>0.0001[a]	0.001[a]	0.0001[a]	0.03[a]	–
Gray Kingbird	Dmax	0.20	0.28	0.22	0.33	0.08	0.51	0.28	0.21
	Significance	0.98	0.32	0.31	0.02[a]	1.53	0.0002[a]	0.08	0.06
Puerto Rican Spindalis	Dmax	0.54	0.05	0.03	–	0.20	0.24	–	–
	Significance	0.22	1.95	1.97	–	1.13	0.74	–	–
Greater Antillean Grackle	Dmax	0.37	0.27	0.20	0.25	0.43	0.57	0.18	0.32
	Significance	0.03[a]	0.06	0.29	0.03[a]	0.001[a]	0.0001[a]	0.32	0.0001[a]
Red-legged Thrush	Dmax	0.17	0.33	0.18	0.17	0.64	0.67	0.93	0.34
	Significance	1.43	0.9	1.20	1.39	0.001[a]	0.002[a]	0.001[a]	0.87
Northern Mockingbird	Dmax	0.26	0.09	0.07	0.06	0.20	0.18	0.50	0.25
	Significance	1.01	1.81	1.91	1.92	0.78	1.71	0.10	0.11

[a] $P < 0.05$, Kolmogorov–Smirnov two-sample test.

[b] See Table 4 for scientific names.

colony edge, and two solitary nests ($d_{max} = 0.865$, $P < 0.0001$, Kolmogorov-Smirnov 2-sample test).

Protection against parasitism by association with an aggressive species.—Yellow Warbler nests ($n = 8$) within 10 m of active Gray Kingbird nests (the distance within which the kingbird maintained high aggression toward cowbirds; Table 6) had a lower incidence of cowbird parasitism (2 nests parasitized) than birds ($n = 79$) nesting beyond 10 m of kingbird nests (63 nests parasitized, 16 not parasitized; $\chi^2 = 11.524$, $P < 0.001$).

DISCUSSION

Anti-parasite aspects of habitat selection.—Birds use visual aspects of the vegetational configuration to select their habitat (Shugart and Patten 1972, Smith 1977). An important aspect of avian nesting habitat is cover, which provides nests with some protection against depredation (Odin 1957, Chesness et al. 1968, Ricklefs 1969, Dwernychuk and Boag 1972, Jones and Hungerford 1972, Collias and Collias 1984, Martin and Roper 1988). Nest predator avoidance, all other factors being equal, results in increased productivity and thus there is a selective advantage in placing nests in cryptic sites. Similarly, birds choosing camouflaged nesting sites should benefit by avoiding brood parasitism. Indeed, several workers have reported that nest predators and brood parasites have coincidental preference for particular habitat features (Donovan et al. 1997, Tewksbury et al. 1998, McLaren and Sealy 2000). Exposed nests would be more easily discovered by vigilant parasites and, given that brood parasitism generally depresses reproductive productivity (Payne 1977, Wiley 1985, Woodworth 1997, Massoni and Reboreda 2002), there should be strong selection for the use of concealed sites.

Other observers have noted habitat differences that affected brood parasitism rates (Hudson 1870, Berger 1951, Gochfeld 1979). Non-parasitized nests of Yellow Warblers in Puerto Rico were more often in sites having greater cover advantage than parasitized nests. Parasitized nests were placed higher in a tree or bush, and in sparser stands of vegetation, and thus probably were more visible to avian nest predators and brood parasites. Non-parasitized nests were typically in smaller trees characteristic of the dense, seral growth of the regenerating forest. In contrast to my observations, Briskie et al. (1990) found that Yellow Warbler nests placed at lower heights in the vegetation were more frequently parasitized in southern Manitoba. Ortega and Ortega (2000), however, found no difference in nest height between nonparasitized and parasitized Yellow Warbler clutches and between depredated nests and those nests not depredated in southwestern Colorado.

The discriminant function for separating parasitized from non-parasitized Yellow-shouldered Blackbird nests was not significant, perhaps because of the small sample size of non-parasitized nests, the blackbird's wide range of habitat use among the variables I measured, and the cowbird's effective penetration of all nesting habitats. Parasitized nests tended to be placed higher in the vegetation and closer to the center of the tree or bush than non-parasitized nests. Lower, distal from trunk, leafy sites typically provide greater vegetative cover than the more open interiors or tops of mangroves.

I compared the number of cowbird eggs laid per nest with habitat variables. Because more than one female cowbird is typically responsible for the multiple parasitism of nests (Hoy and Ottow 1964, J. W. Wiley, pers. obs.), I suspected that a nest's susceptibility to parasitism might be reflected in the number of cowbird eggs deposited; i.e., the number of cowbird eggs should be negatively correlated with habitat parameters that provide some degree of cryptic advantage to a nest. My analysis of nest site data, however, revealed no clear pattern of host habitat selection against parasitism. The results suggest that Yellow-shouldered Blackbird nests in denser shrub stands were parasitized by fewer cowbirds than those nests in more open vegetation. Analysis of number of Shiny Cowbird eggs in parasitized Yellow Warbler nests yielded results that supported the discriminant function; i.e., lower-placed warbler nests (hence denser canopy camouflage from surrounding vegetation) had fewer parasite eggs, possibly because cowbirds found these nests less often than higher-placed nests.

Egg-eating birds sometimes use a silent "watch-and-wait" strategy to locate active nests (Hammond and Forward 1956, J. W. Wiley pers. obs.), similar to the cryptic vigilance I observed Shiny Cowbirds using to locate potential host nests (Fig. 2A; Wiley 1982). Therefore, use of some cover components of the habitat may be effective in avoiding both nest depredation and brood parasitism. Placement of nests in dense vegetation may be important in avoiding the active or systematic search strategy occasionally used by Shiny Cowbirds (and predators; Wiley 1982). Brood parasites systematically searching vegetation may be more likely to move through those sections offering a clear pathway; i.e., they may avoid the denser foliage of the distal portions of branches. In denser vegetation, cowbirds may be at greater risk to host aggression, by not being able to visually determine if a potential host is at the obscured nest or nearby. Successful nesting Yellow Warblers used habitat components I judged important in camouflaging nests from predators and parasites; i.e., nests placed in low, dense, mid-seral stages of shrub and tree stands, with complete canopy cover. However, I found no relationship between the habitat variables measured and nest success for Yellow-shouldered Blackbird.

It could be argued that the distribution of the non-parasitized or successful nests of warblers and blackbirds merely represents nest site correlation rather than true nest selection (Wiens 1976). Do the nest sites represent a preference, or is the correlation of an individual's presence with certain habitat components the result of the operation of extrinsic forces? Because blackbirds and warblers site their nests in a broad range of habitats, pairs would be expected to vary in their abilities to avoid predators or brood parasites as related to cryptic elements in their nest habitat. In the early stages of host-parasite interactions in Puerto Rico, hosts may not select habitat in avoidance of parasites. Rather, the observed correlation may be among certain aspects of habitat incidentally effective in avoiding parasites and the improved reproductive success of those pairs using these habitat components. Nevertheless, considering the observed range of host usage within habitat components and evidence that some of these components may be effective in parasite avoidance, the potential exists for selection of microhabitats important in a nest concealment strategy for parasite evasion.

I concluded that similar habitat components for cover are important in both predator and parasite avoidance. This suggests that anti-predator strategies of cover usage may be a preadaptation to anti-parasite strategies. If so, many of the behavioral mechanisms for brood parasite avoidance may already exist in some nesting bird populations recently exposed to social parasitism. Evolution of improved anti-parasite strategies through use of cover might be expected to occur at a rapid rate with the strong selective advantage of improved nest success and productivity at non-parasitized nests. Of course, there is also strong selective advantage for the parasites to evolve effective mechanisms for finding host nests. Thus, there would be a series of strategies and counter strategies evolving in the population affected by cowbird parasitism.

Host discrimination.—In parts of its range where Yellow Warbler has long been exposed to Brown-headed Cowbird parasitism, burial is the host's most common response to a cowbird egg (Briskie et al. 1992, Sealy 1995). In Ontario, almost half (48%) of the parasitized Yellow Warbler nests studied by Clark and Robertson (1981) were built-over by the host. Burgham and Picman (1989) found egg burial was a frequent response by Yellow Warbler to Brown-headed Cowbird parasitism in eastern Ontario, where cowbirds had only recently expanded their range. I observed an egg burial rate of about 2.5% at nests of two regular host species in Puerto Rico, despite the cowbird's common habit of depositing eggs in nests before hosts laid their own eggs. As in other studies (Rothstein 1975a, Clark and Robertson 1981), egg burial in the Puerto Rican host populations occurred at the early egglaying stage. This supports the hypothesis that the cowbird may have miscued on nest completion and deposited its egg before the host had finished nest building (Rothstein 1975a). Clark and Robertson (1981) found that parasitized nests in which hosts buried alien eggs had success rates comparable to unparasitized nests, a situation that would tend to reinforce burial behavior. At all Puerto Rican nests in which alien eggs were buried and hosts laid their eggs on the new nest floor, cowbirds also laid additional eggs, so no fitness gain was achieved by the hosts. If egg burial does not result in greater nest success among host populations in Puerto Rico, this behavior would not be expected to become more common as an anti-parasite adaptation. Twenty years after my observations, however, Vincenty *et al.* (2009) found a substantial increase in the incidence of egg burial at warbler nests in the Boquerón region; in 2000 and 2001, 29% of Yellow Warbler nests examined had egg burials, indicating a considerable increase in that host species' discriminatory behavior.

Under normal circumstances, eggs remain stationary in the proper nest. Thus, for birds not exposed to brood parasites, there has not been prior selection to enhance discrimination in egg recognition (Hamilton and Orians 1965). Rothstein (1975a) suggested that nest desertion and egg burial may not be anti-parasite adaptations, but by-products of standard avian behavior patterns. Egg ejection, however, was most reasonably interpreted as an evolved anti-parasitized defense. Therefore, ejection behavior would not be expected in a population only recently exposed to cowbird parasitism. Nevertheless, I found that several species in Puerto Rico eject alien eggs from their nests.

Certain species may have some preadaptive behavior for discriminating between their own and alien eggs. Pearly-eyed Thrashers (*Margarops fuscatus*) commonly take over nesting cavities from other species and, in doing so, eject or eat the evicted resident's eggs (Arendt 2006, J. W. Wiley pers. obs.). Thrashers may have developed discriminating abilities to avoid mistakes in eating or ejecting their own eggs after nesting take-overs, traits for which there must be extremely high selective value. Red-legged Thrushes and Northern Mockingbirds are occasional egg predators (J. W. Wiley pers. obs.) and similarly may have developed inhibitory behavior to avoid mistakenly destroying their own eggs. Many species are known to "dump" eggs in the nests of other conspecifics, although the extent of this behavior is not known for most species (Wiens 1965, 1971, Holcomb 1967, Cannell and Harrington 1984, Carter 1987, Sealy 1989). The ability to discriminate among one's own eggs and those of another individual would have the selective advantage of ensuring the nest owner's genes were more likely to survive.

Similar to my observations for the avian communities in Puerto Rico, Rothstein (1975a) found no strong relationship between intensity of Brown-headed Cowbird parasitism and response to that parasitism. Therefore, he rejected the prediction that acceptors should be subject to little or no parasitism and rejectors to occasional or heavy parasitism.

Rejection behavior would have no adaptive value if a host and its offspring suffered no harmful effects from parasitism. Rothstein (1975a) found that both rejector and acceptor species within the range of Brown-headed Cowbird were harmed by cowbird parasitism. In Puerto Rico, two acceptor species (Black-faced Grassquit *Tiaris bicolor* and Nutmeg Mannikin *Lonchura punctulata*) were not observed to be parasitized, whereas Greater Antillean Grackles did not exhibit reproductive losses at parasitized nests (Wiley 1985). All other acceptor species were adversely affected (lowered nest success and productivity) by parasitism, although the effects were less clear for Yellow Warbler and Yellow-shouldered Blackbird, where nest success did not differ between parasitized and non-parasitized nests (Wiley 1985). Nevertheless, numbers of host chicks fledged per parasitized nest were lower than at unparasitized nests (Wiley 1985).

Species that regularly eat eggs of other birds might easily evolve rejection behavior, because they already have motor skills needed to manipulate eggs. Rothstein (1975a) found this to be true for hosts of Brown-headed Cowbird. I found the hypothesis also valid for Puerto Rican host species, where the rejectors Pearly-eyed Thrasher and Red-legged Thrush are egg predators (Wiley and Wiley 1979, J. W. Wiley unpubl. data). However, Greater Antillean Grackle, an acceptor species, also occasionally robs eggs.

All alien egg rejections by Bananaquits (*Coereba flaveola*) were by nest desertion. This reaction to the cowbird egg could be adapted from evolved defense to other situations wherein nest desertion would be favorable; e.g., desertion after a nest has been disturbed by a predator. Cowbird egg rejection from the Bananaquit's enclosed, globular nest might be physically impossible for the Bananaquit with its specialized bill.

Post and Wiley (1977b) estimated that Shiny Cowbird arrived in Puerto Rico in the 1940s or early 1950s, judging from documented sighting locations, population trends of its major host (Yellow-shouldered Blackbird), and cowbird invasion patterns on other islands. Rothstein (1975a) calculated that populations parasitized by Brown-headed Cowbirds would require from 20 to 100 years to go from 80% acceptance to 80% rejection rates of cowbird eggs. Presumably there must also be a period when the rejection rate is at zero before the trait makes its initial appearance in the parasitized population. Once the trait appears, the population would rapidly approach fixation for rejection because of its extraordinary high selective value (Rothstein 1975c).

Nesting bird populations in Puerto Rico may have met the minimum number of years of exposure to cowbird parasitism required to achieve the high rejection rates I observed in the 1970s and 1980s, however other circumstances confound this possibility. Each of the several species that exhibit rejection behavior was at that time incurring low, or no, parasitism. This may be related to the species' rejection behavior, but several other characteristics shown by these populations reduce the chances of their nests being parasitized. For example, some species are poor hosts because of suitability of food delivered to nestlings (Wiley 1982). The egg of Red-legged Thrush is much larger than that of Shiny Cowbird, which may affect hatchability of the cowbird's egg in the thrushes' nest (Wiley 1982). Some species are extremely aggressive at their nests or exhibit high attendance rates, making it unlikely that cowbirds could penetrate their defenses to lay eggs. Because of the low parasitism rates at such nests, the selective pressures of parasite-affected productivity loss in the host also would be low. Hence, evolution of a rejection trait within an irregularly parasitized population might take considerably longer than for a host population under extreme selective pressure.

Nest guarding and aggression as anti-parasite strategies.—Other studies have shown nest guarding to be an important deterrent to intra- and interspecific nest parasitism in birds (Møller 1987, 1989; Mermoz and Fernández 1999; but see Olendorf and Robinson 2000). Based on my observations, I concluded that nest attentiveness was important in countering brood parasitism, and those species most diligent in nest guarding during egg laying experienced less parasitism than species showing low attendance. When a potential host is on its nest, little chance exists for a parasite to lay its egg. Thus, a strong selective advantage to close nest guarding would be expected among species that are regularly parasitized. A brood parasite normally waits until the host has left its nest before visiting (Hudson 1870, Payne 1977), thereby minimizing risk of injury from an encounter with an aggressive host (Fig. 2F). Although Hudson (1870) reportedly never saw cowbirds force hosts from nests, others have observed cowbirds using aggressive supplantation to enter host nests (e.g., Ovenbird *Seiurus aurocapilla*, Hann 1937; Yellow Warbler, this study). Such interactions are apparently uncommon and have involved hosts smaller than the parasite. It would be maladaptive for the cowbird to develop a strategy of supplanting certain host species from their nests because of the risk of physical injury from combat between a larger host and the parasite. Mason (1987), however, reported groups of up to four Shiny Cowbirds searching for host nests. I also observed groups of up to four cowbirds (one male and three females) apparently exploring nesting habitat and such groups may be effective in flushing even larger hosts from nests, thereby allowing unchallenged or low-risk entry.

Anti-predator behavior at nests is a probable preadaptation to defense against brood parasites. It is adaptive to chase certain egg or chick predators from one's nest; e.g., increased nest defense by Stonechats (*Saxicola torquatus*; Greig-Smith 1980) and Eastern Kingbirds (*Tyrannus tyrannus*; Blancher and Robertson 1982) has been shown to decrease depredation at nests. A non-discriminating, aggressive individual may defend its nest against all intruders, including cowbirds, and should benefit from resisting brood parasitism. Hence, the consistently high aggression toward non-cowbird species I observed among the several non-parasitized species may serve as a preadaptation to counter brood parasitism. Nevertheless, there must be a limit to benefit gained relative to energy expended in supplanting all species from nesting areas. It would be advantageous to the individual to develop discriminatory capabilities so that energy is not wasted in chasing species that are not threats to breeding efforts. Thus, kingbirds may ignore such species as Bananaquits because they do not threaten the nest structure or its contents, nor are they niche competitors. Conversely, the kingbird may develop increased awareness and aggressiveness toward species of actual competitors or predators; e.g., grackles which are egg robbers and that steal nesting material from kingbirds.

In Puerto Rico, I found that species or individuals displaying the highest aggression rates had the lowest levels of parasitism. The aggressive behavior of these species (or individuals) was apparently effective in fending off attempts by cowbirds to enter the hosts' nests. Even among species that were occasionally or regularly parasitized (11–100% of nests parasitized; = "Acceptors"), I found that, overall, there was a moderate negative association of aggression with the rate of parasitism. Robertson and Norman (1977) and Folkers (1982) systematically investigated nest guarding among bird populations with long histories of brood parasitism by Brown-headed Cowbirds. They, too, found differences in host behavior toward cowbirds between parasitized and of non-parasitized species. Within a taxon, the intensity with which acceptor species reacted to cowbirds was proportional to the intensity of parasitism experienced by each species.

In contrast to some non-parasitized nesting species that were equally aggressive toward all invaders, including cowbirds, regularly parasitized species in Puerto Rico responded differently toward cowbirds than to other intruding species. This suggests that those host populations are capable of developing skills in discrimination. Such skills could be adaptive responses to the strong selective pressure of reproductive losses at parasitized nests. Some species that were not regularly parasitized had certain preadaptations that served to counter parasite activity (high nest attendance or aggression toward all intruders) and, thus, there was apparently little selective pressure resulting from parasitism to reinforce discriminatory responses to cowbirds. Other non-parasitized species, however, did exhibit elevated responses to cowbirds. These may have been learned responses resulting from persistent attempts by cowbirds to enter nests. Other intruding species may be less persistent and thereby offer fewer learning opportunities.

Avian populations in Puerto Rico have had little time to develop innate responses to counter parasitism. Nevertheless, there must be strong selective advantage for parasitized individuals to develop anti-cowbird strategies and for such mechanisms to quickly become fixed in the population. Learned responses may have been displayed by some species as early as the 1970s, judging from the differences in aggressiveness I observed among several host and non-host species. Perhaps these species have different learning abilities for discriminating between intruders which, in combination with the differences in cowbird preferences for hosts and effectiveness of preadaptive mechanisms within the behavioral repertoire of a species, may account for much of the variation I observed in parasitism rates among species.

Given time to evolve, regularly parasitized species in Puerto Rico would be expected to develop elevated levels of aggression toward the brood parasite, similar to the situation reported by Robertson and Norman (1977) and Folkers and Lowther (1985). Yellow Warbler, which in Puerto Rico showed much lower aggression toward cowbirds than toward other intruding species, displayed greater aggressiveness toward parasites than non-parasites in parts of its North American range where it has had a long history of association with a brood parasite (Robertson and Norman 1977, Folkers 1982, Folkers and Lowther 1985). Even North American Yellow Warbler populations only recently exposed to Brown-headed Cowbird populations recognized the parasite as a specific threat to their nests (Burgham and Picman 1989). Increased aggressiveness, however, has disadvantages. In low-density host populations, cowbirds may use aggression as a nest-locating cue, because where few nesting individuals occur there may be too few neighboring hosts to mount an effective multi-species mobbing response (Robertson and Norman 1977). Although aggressive behavior is maladaptive in low-density nesting populations, Robertson and Norman (1977) presented evidence for the evolution of increased aggression because host individuals breeding in denser populations were found to have greater fitness.

Whereas Greater Antillean Grackle was determined to be an egg acceptor and spent considerable time away from its nest, the incidence of nest parasitism within nesting colonies of this species was low. This may be attributable to the vigilance and aggressiveness of neighboring grackle pairs that, while defending their own nests, incidentally guarded an absent grackle pair's nest against cowbird entry. Such breeding congregations of aggressive birds could give an individual considerable protection against cowbird parasitism. Even when a pair leaves its nest to forage, vigilant nesting neighbors would incidentally guard nearby nests from cowbird entry (for colonial nesting grackles, the defended area had a radius of 10–20 m; Table 6). Friedmann *et al.* (1977) suggested that colonially nesting Common Grackle (*Quiscalus quiscula*), an acceptor species, may escape brood parasitism incidental to neighboring pairs defending unguarded nests within their territories. Similarly, colonially nesting Tricolored Blackbirds (*Agelaius tricolor*) were not parasitized, whereas Red-winged Blackbirds (*A. phoeniceus*), nesting non-colonially, were parasitized by Brown-headed Cowbird (Payne 1973). Yellow-winged Blackbirds (*A. thilius*) benefit by nesting close to one another through reduced brood parasitism by Shiny Cowbird (Massoni and Reboreda 2001).

I found that Yellow Warblers nesting within the "response range" (Clark and Robertson 1979) of nesting Gray Kingbirds incurred lower cowbird parasitism rates than did warbler nests outside that range. The kingbird, a larger, highly attentive, and aggressive species, effectively defended warbler nests from cowbird parasitism, while driving the parasites from kingbird territories. Clark and Robertson (1979) found that nesting Yellow Warblers apparently benefitted from the Gray Catbird's (*Dumetella carolinensis*) nest-guarding behavior and aggressive responses to predators. They also found a significantly lower incidence of brood parasitism occurring at Yellow Warbler nests that were in a Red-wing Blackbird's response range. Overall, Clark and Robertson (1979) found that warblers nesting within the response range of blackbirds had higher nest success than other Yellow Warblers. Advantages in nesting close to an aggressive species have also been proposed for other species (Wiley and Wiley 1979).

SUMMARY AND CONCLUSIONS

I found that (1) certain habitat components may be effective in concealing nests from brood parasites, with some of these components similar to those important in evading nest depredation; (2) breeding species in Puerto Rico are divisible into rejectors and acceptors of cowbird eggs, with regularly parasitized species being acceptors, whereas non-parasitized or infrequently parasitized species were characteristically rejectors; and (3) nest guarding is an effective strategy in countering brood parasitism. Species displaying high nest attentiveness and aggressiveness toward cowbirds have a low incidence of parasitism.

Shiny Cowbird, which recently arrived in Puerto Rico via a northward range expansion, has a wide array of potential hosts from which to choose. Within that array, some species were initially unavailable as hosts because of certain physical (e.g., body and egg size differences), behavioral (nest guarding), or ecological (food differences) factors. Other species with certain preadaptations (mainly anti-predator) incidentally effective in resisting parasitism have not been parasitized or suffer only low intensities of parasitism. Populations of nesting species not exhibiting these characteristics have been heavily parasitized (Wiley 1985).

The avian community in Puerto Rico evidently had no previous exposure to brood parasites and, therefore, no battery of specific anti-parasite defenses was available. Still, several anti-predator preadaptations have been effective (directly or with some modification) in resisting parasitism. Learned defense responses against cowbirds may already be developing within some populations (e.g., differential nest defense behavior toward cowbirds compared with other intruding species).

Populations of regularly parasitized host species are expected to decline because of reduced nest success and productivity caused by cowbird parasitism. These consequences place high selective values on the development of behavioral and ecological defenses, particularly among those host populations most severely exploited by cowbirds. In the future, specific anti-parasite strategies should evolve within the avian community, through modification of existing behavior or evolution of new mechanisms to counter parasitism. Along with the evolution of effective anti-parasite mechanisms by host populations, however, Shiny Cowbirds will likely coevolve means to circumvent these defenses, resulting in an escalating series of counter tactics toward an evolutionarily stable strategy (Mason and Rothstein 1986).

The data reported here were collected in the 1970s and early 1980s, and are among the earliest observations on Shiny Cowbird-host interactions in Puerto Rico. As such, these data can serve as baselines against which changes in host and parasite behavior and ecology can be measured over time (López-Ortiz *et al.* 2006, Vincenty *et al*. 2009). Further, these data can be used to gauge the effectiveness of management efforts to control Shiny Cowbirds in Puerto Rico (Cruz *et al.* 2005).

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