

PATTERNS OF SHINY COWBIRD PARASITISM IN ST. LUCIA AND SOUTHWESTERN PUERTO RICO¹

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Abstract. The density of Shiny Cowbirds (*Molothrus bonariensis*) in lowland St. Lucia and Martinique is about six individuals/km², compared to 49/km² in lowland southwestern Puerto Rico. Their distribution in the Antilles may be related to agriculture that provides food for adults, as much as to availability of suitable hosts. In St. Lucia, four of eight potential host species were parasitized. Black-whiskered Vireos (*Vireo altiloquus*) and Yellow Warblers (*Dendroica petechia*) accounted for 90% of all parasitized nests. Patterns of parasitism did not match host availability in either SW Puerto Rico or St. Lucia. In St. Lucia only Gray Kingbirds (*Tryannus dominicensis*) rejected >75% of experimental cowbird eggs. Gray Kingbirds, Northern Mockingbirds (*Mimus polyglottos*), and Greater Antillean Grackles (*Quiscalus niger*) were rejecters in Puerto Rico. The success of parasitized Yellow Warbler nests was higher in Puerto Rico than in St. Lucia. Cowbird parasitism reduced Yellow Warbler nest success in St. Lucia, but not Puerto Rico. Comparisons with Puerto Rico indicate that neither hosts nor cowbirds in St. Lucia have evolved defenses or counter-defenses during a 40-year period.

Key words: Brood parasitism; host selection; egg rejection; Shiny Cowbird; *Molothrus bonariensis*; St. Lucia; Puerto Rico; Martinique.

INTRODUCTION

The Shiny Cowbird (*Molothrus bonariensis*), a generalist brood parasite, has spread rapidly northwest through the Caribbean (Post and Wiley 1977a), reaching North America by 1985 (Smith and Sprunt 1987). In the Antilles, the cowbird has lowered the reproductive output of several host species (Post and Wiley 1977b, Post 1981, Wiley 1985, Cruz et al. 1989). Although cowbird-host relationships are now fairly well-known in the Greater Antilles (Post and Wiley 1977a, 1977b; Arendt and Vargas Mora 1984; Wiley 1985, 1988; Perez-Rivera 1986; Cruz and Wiley 1989; Cruz et al. 1989), little is known about them in the Lesser Antilles.

We compared parasite-host relationships in two areas of the Caribbean, where the cowbird has occurred for different lengths of time. It has been in St. Lucia since at least 1931 (Danforth 1932). It was first reported from southwestern Puerto Rico about 1969 (Post and Wiley 1977a). Our

objectives were to: (1) contrast the distribution and abundance of Shiny Cowbird populations in St. Lucia and Martinique with similar populations in SW Puerto Rico, (2) describe differences in rates of parasitism of similar bird communities in St. Lucia and SW Puerto Rico, and (3) compare cowbird egg rejection and nest abandonment in experimentally parasitized hosts in St. Lucia and SW Puerto Rico.

STUDY AREAS AND METHODS

We examined the distribution and reproduction of Shiny Cowbirds in dry coastal lowlands and coastal hills in southwestern Puerto Rico and southern St. Lucia. Both areas represented a composite of habitats, from pastures with scattered trees to dry woodland with emergent trees. The impact of stock grazing and wood cutting is severe in many areas, as reflected by the dominance of ruinate and scrub. Most areas protected from grazing were in succession, and appeared as intermittent patches of scrub. Even though southern St. Lucia is wetter (average annual rainfall = 122 cm, falling mainly June–November) than SW Puerto Rico (annual rainfall = 72 cm,

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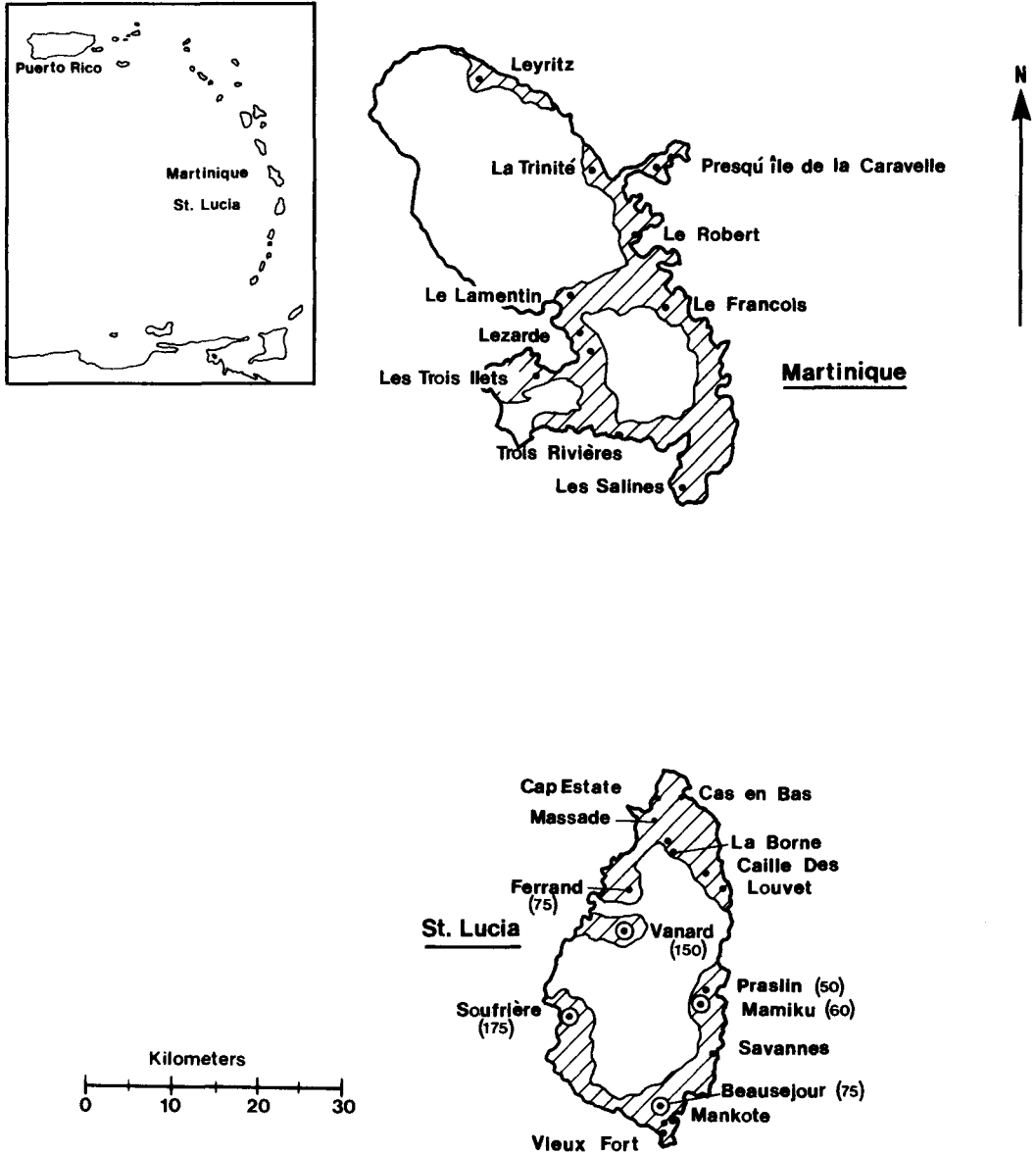


FIGURE 1. St. Lucia and Martinique. Dots are locations of transects. Circles around dots indicate regularly used feeding sites of Shiny Cowbirds. Numbers are estimated sizes of flocks. Cross-hatched areas represent lowland zones that were searched for Shiny Cowbirds.

mainly in April–June), the influence of the trade winds, and the dominance of disturbance-selected plants at the former site have favored epharmonic convergence with the Puerto Rican site.

Studies in St. Lucia were concentrated around Hewanorra Airport near Vieux Fort, the Mankote Swamp, and in dry forest in the coastal hills

(Mt. Tournay, Mt. St. Urbain, and Halycon Hill, all less than 150 m high). In SW Puerto Rico we worked in the Boquerón Commonwealth Forest and adjacent lands, between La Parguera and El Combate (see maps in Post 1981).

We surveyed five habitat types for nesting passerines: (1) Mangrove (*Avicennia germinans* and *Rhizophora mangle*) and mangrove edge. (2) Ag-

ricultural lands and pastures with scattered trees and shrubs. These included coconut (*Cocos nucifera*) plantations in St. Lucia and subsistence farm plots in Puerto Rico. (3) Dry scrub, usually dominated by mesquite (*Prosopis pallida*), *Acacia* spp., and logwood (*Haematoxylum campechianum*). (4) Littoral strand vegetation containing mainly spurges and forbs (Euphorbiaceae and Verbenaceae) in St. Lucia and scrub (Polygonaceae spp.) in Puerto Rico. (5) Dry forest woodland with sclerophyllous trees (≤ 10 m high) and a well-developed scrub understory. In Puerto Rico, this habitat was dominated by oxhorn buccida (*Bucida buceras*), gumbo-limbo (*Bursera simaruba*), lignum-vitae (*Guaiacum officinale*), and mesquite. Dry woodland in St. Lucia was floristically similar to Puerto Rico, with the addition of *Lonchocarpus* spp., a greater abundance of white-cedar (*Tabebuia heterophylla*), and the deletion of lignum-vitae.

Study in St. Lucia was undertaken during 23–25 March 1982, 29 May–23 June 1983, 22 June–15 August 1984, and 16 June–3 September 1985. Comparative data were gathered in Martinique 7–25 December 1981, 19–21 March 1982, and 15–17 July 1984, and in Puerto Rico 1 January–27 June 1982, 30 April–30 November 1983, and 16 September 1986–8 August 1987.

To determine the abundance of cowbirds and other species, we established transects, at least 0.5 km long, along existing paths or narrow roads. All census plots were in structurally similar habitats on each island. We determined island-specific aural detection distances for each species on each island. After these distances were plotted as perpendicular distances from the transect, we determined an inflection point for each detection curve (Emlen 1971, 1977, 1984). The distance to the inflection point defined the width of the species-specific census plot on the respective island. All adult individuals were recorded. In St. Lucia, 25 censuses were conducted at 18 sites (Fig. 1) (mean length = 1.1 km, range = 0.5–2.6 km). In Martinique, bird densities were measured at nine sites, mainly in the nonmountainous southern and eastern sections of the island (Fig. 1). The mean length of the 12 transects was 1.5 km (range = 0.5–2.6 km). The Puerto Rico study site was in and around Boquerón Commonwealth Forest, from La Parguera to Las Palmas (see maps and photographs in Post 1981 and Post and Wiley 1976). In Puerto Rico, the mean length of the 18 transects, conducted at 12

sites, was 1 km (range = 0.5–2.1 km). Post conducted all censuses between dawn and 12:00.

We estimated nest density assuming that the populations we studied were predominately monogamous, an assumption based on our own observations and on published reports. Total density of parasitized nests in each area was calculated by multiplying number of pairs per km² of each species by the species-specific parasitism rate, and summing over all species.

We searched the study areas daily for nests. Nests were marked with numbered tags, placed inconspicuously nearby, and were checked every 3–4 days. If the nest failed, we attempted to determine why, using criteria similar to those of Wiley (1985). A nesting attempt was considered successful if one or more young fledged. Young which disappeared from the nest after the 12th day were assumed to have fledged (mean nesting period for all species was 11.3 days). Data on nests containing cowbird eggs but no host eggs were included in the determination of parasitism rates, but were not used for calculations of host nest success. These nests constituted less than 3% of the nest sample.

We followed Rothstein's (1971) method of experimentally parasitizing nests. Eggs were shaped from plastic wood putty and painted with acrylic paint to resemble real cowbird eggs. Nests were artificially parasitized during the egg-laying period, or during the first 3 days of incubation, between dawn and mid-morning. We considered eggs rejected if they disappeared from the nest, or if the nest was deserted (nest contents intact, but the eggs cold, and hosts not attending the nest). If a nest was depredated before the 5th day following artificial parasitism, we did not include it in the analysis.

RESULTS

ABUNDANCE AND DISTRIBUTION OF SHINY COWBIRDS

Cowbirds in St. Lucia occurred at highest densities during the dry season, where they aggregated at pigstys, poultry barns, and a brewery. About 175 cowbirds were at a poultry farm in Soufriere (Fig. 1), representing the largest concentration at all surveyed feeding sites. The total minimum number of cowbirds estimated at seven widely spaced feeding locations was 585. The largest concentration of cowbirds seen in St. Lucia, 209 individuals, was in a communal roost at the southern end of the island. During the

TABLE 1. Densities of the Shiny Cowbird and its actual and potential hosts, and prevalence of cowbird parasitism in St. Lucia and Puerto Rico. Data for St. Lucia collected in 1984–1985 and for Puerto Rico in 1982–1983 and 1986–1987.

Species	St. Lucia (25) ^a		Puerto Rico (18)	
	No. birds per km ²	% parasitism (n) ^b	No. birds per km ²	% parasitism (n)
Shiny Cowbird	6.2	—	49.3	—
Known hosts: ^c				
Caribbean Elaenia	109.0	9.5 (21)	73.5	—
<i>Myiarchus</i> spp. ^d	0	—	61.7	22.6 (31)
Gray Kingbird	17.6	0 (8)	65.0	0 (29)
<i>Turdus</i> spp. ^e	12.7	0 (17)	0	0 (3)
<i>Mimus</i> spp. ^f	14.4	0 (42)	71.6	0 (15)
<i>Margarops</i> spp. ^g	37.9	0 (15)	0	—
Black-whiskered Vireo	27.2	87.5 (24)	24.2	72.7 (11)
Yellow Warbler	23.1	55.2 (29)	132.0	22.2 (45)
Adelaide's Warbler	55.0	0 (10)	150.5	12.5 (8)
Yellow-shouldered Blackbird	—	—	66.9	96.8 (93)
<i>Quiscalus</i> spp. ^h	80.6	1.7 (115)	16.5	4.1 (49)
<i>Icterus</i> spp. ⁱ	4.9	—	24.0	—
Estimated density of known hosts (individuals/km ²)	382.4		685.9	
Not known as hosts:				
Bananaquit	84.9	0 (30)	165.2	0 (24)
Streaked Saltator	32.3	0 (33)	—	—
Black-faced Grassquit	103.0	0 (41)	75.2	0 (15)
<i>Loxigilla</i> spp. ^j	85.6	0 (34)	6.3	0 (4)
Estimated density of parasitized nests/km ^{2k}	24.3		72.5	

^a Number of transects.

^b Number of nests examined.

^c At least one reported instance of Shiny Cowbird parasitism in the Antilles.

^d Puerto Rican flycatchers in Puerto Rico and Lesser Antillean Flycatchers (*M. oberi*) in St. Lucia.

^e Bare-eyed Thrushes in St. Lucia and Red-legged thrushes in Puerto Rico.

^f Northern Mockingbirds in Puerto Rico and Tropical Mockingbirds in St. Lucia.

^g Scaly-breasted Thrashers in St. Lucia and Pearly-eyed Thrashers in Puerto Rico.

^h Greater Antillean Grackles in Puerto Rico and Caribbean Grackles in St. Lucia.

ⁱ St. Lucia Orioles in St. Lucia and Troupials in Puerto Rico.

^j Puerto Rican Bullfinches in Puerto Rico and Lesser Antillean Bullfinches in St. Lucia.

^k Calculation based on population density of host pairs, weighted by parasitism rate (see Methods).

breeding season cowbirds were less often seen in farmyards, and usually fed in small flocks of 10 or fewer birds in pastures and other disturbed habitats.

We found no large feeding flocks of cowbirds in Martinique. Eleven individuals, the most in one area, were seen at a dairy farm near Francois (Fig. 1). Ten more cowbirds were roosting with Caribbean Grackles (*Quiscalus lugubris*) at Lamentin, near the coast. We monitored other roosts, which had up to 500 Caribbean Grackles, but found no other cowbirds. Most cowbirds recorded on transects were in or near mangroves or strand habitats on the southern end of Martinique. The densities of cowbirds in St. Lucia and Martinique, as determined by transects, were about six individuals per km², 12% the estimated density in Puerto Rico.

In contrast to the Lesser Antilles, we found larger flocks of cowbirds in Puerto Rico, mainly in mixed-species roosts at Pita Haya, at the western edge of the study site, and in Bahía Sucia, 2 km to the west. The most counted at these roosts were 448 and 782, respectively. The largest concentration of cowbirds reported from the southwestern coast of Puerto Rico, 4,299, was in a September 1973 roost near Isla La Cueva, 2 km east of the study area (Post and Post 1987).

HOST SELECTION BY SHINY COWBIRDS

On our study sites in St. Lucia and Puerto Rico we identified 11 species or genera that are known to have been parasitized by Shiny Cowbirds in the Caribbean (Table 1; Friedmann et al. 1977, Friedmann and Kiff 1985, Wiley 1985). In St. Lucia the main hosts, Yellow Warblers (*Den-*

TABLE 2. Reproductive success of Shiny Cowbirds in 1984–1985 in St. Lucia and in 1982–1983 and 1986–1987 in SW Puerto Rico. Numbers in parentheses indicate number of nests examined.

Locality	Host	No. of Shiny Cowbird eggs/nest	No. of Shiny Cowbird fledglings/nest
St. Lucia	Caribbean Elaenia	1.00 ± 0 (2)	0.50 ± 0.71 (2)
	Black-whiskered Vireo	1.33 ± 0.48 (21)	0.42 ± 0.51 (21)
	Yellow Warbler	1.31 ± 0.60 (16)	0.13 ± 0.35 (15) ^a
	Carib Grackle	1.00 (1)	1.00 (1)
	Total	1.29 ± 0.51 (40)	0.35 ± 0.48 (39)
Puerto Rico	Puerto Rican Flycatcher	1.33 ± 0.52 (6)	0.50 ± 0.55 (6)
	Black-whiskered Vireo	1.13 ± 0.35 (8)	0.29 ± 0.49 (7)
	Yellow Warbler	1.00 ± 0 (8)	0.75 ± 0.46 (8) ^a
	Adelaide's Warbler	1.00 (1)	0 (1)
	Greater Antillean Grackle	1.00 ± 0 (2)	0 (2)
	Yellow-shouldered Blackbird	3.74 ± 2.50 (100)	0.79 ± 1.12 (67)
	Total	3.23 ± 2.48 (125)	0.70 ± 1.01 (91)
	Adjusted total ^b	1.12 ± 0.33 (25)	0.45 ± 0.51 (24)

^a A significantly larger number ($t = 3.6$; $P < 0.001$) of cowbird fledglings were produced per nest in Puerto Rico than in St. Lucia.

^b Excluding data from Yellow-shouldered Blackbird nests.

droica petechia) and Black-whiskered Vireos (*Vireo altiloquus*), had intermediate population densities, while the most common passerines, Caribbean Elaenia (*Elaenia martinica*), Carib Grackle, and Adelaide's Warbler (*Dendroica adelaidae*) were little used as hosts.

The three known hosts most common in Martinique, Caribbean Elaenias (46.6 individuals/km²), Yellow Warblers (52.6/km²), and Carib Grackles (127.4/km²), composed 78% of the potential host population in Martinique. The Yellow Warbler, which made up 18% of this population, was the only species that is frequently reported parasitized by the Shiny Cowbird.

Suitable host density in Puerto Rico was 1.8–2.4 × greater than in the Lesser Antilles. As in St. Lucia, we found only a few species parasitized. The four main hosts, the Puerto Rico Flycatcher (*Myiarchus antillarum*), Black-whiskered Vireo, Yellow Warbler, and Yellow-shouldered Blackbird (*Agelaius xanthomus*), made up 42% of the known host population in Puerto Rico, but composed 97% of nests that were parasitized (Table 1).

REPRODUCTION OF SHINY COWBIRDS

The mean number of Shiny Cowbird eggs per nest in St. Lucia (1.29 ± 0.51; $n = 41$) was significantly lower ($t = 5.49$; $P < 0.001$) than in Puerto Rico (3.23 ± 2.48; $n = 124$). However, the higher average number of eggs per nest in Puerto Rico was largely attributable to multiple parasitism of the Yellow-shouldered Blackbird.

When the contribution of parasitism to Yellow-shouldered Blackbird nests was removed, mean number of cowbird eggs per nest was not statistically different between the two islands ($t = 1.48$; $P > 0.05$; Table 2).

Mean number of cowbird fledglings per all parasitized nests in St. Lucia was 0.35 ± 0.48 ($n = 40$), compared to 0.70 ± 1.01 in Puerto Rico ($n = 91$), a significant difference ($t = 4.3$; $P < 0.005$). Again, the higher number of cowbirds fledged per nest in Puerto Rico was related to more cowbird eggs being laid per Yellow-shouldered Blackbird nest. When adjustment was made for cowbirds fledged from blackbird nests, the mean number of cowbirds fledged per nest did not differ between St. Lucia and SW Puerto Rico (Table 2).

A higher incidence of multiple parasitism in SW Puerto Rico may reflect the high relative density of cowbirds. In this area, 74.3% of all parasitized nests contained more than one cowbird egg. Most (96.1%) instances of multiple parasitism were of Yellow-shouldered Blackbirds. In St. Lucia 37.9% of all parasitized nests contained more than one cowbird egg. Most (63.6%) of the multiple-egg nests were those of the Black-whiskered Vireo. Contrasts between islands for rates of multiple parasitism for nonblackbird hosts were not statistically different ($\chi^2 = 2.93$; $0.10 < P < 0.25$).

Although we found no difference between islands for most species in numbers of cowbird eggs or fledglings per host nest, more cowbirds

TABLE 3. Responses of nesting birds to artificial parasitism in 1984–1985 in St. Lucia and in 1982–1983 and 1986–1987 in SW Puerto Rico.

Species	% rejection (no. of tests) in:	
	St. Lucia	SW Puerto Rico
<i>Coccyzus</i> spp. ^a	0 (6)	0 (4)
Caribbean Elaenia	0 (8)	—
Puerto Rican Flycatcher	—	0 (5)
Gray Kingbird	100.0 (2)	100.0 (11)
Caribbean Martin ^b	—	14.3 (7)
<i>Mimus</i> spp.	14.3 (14) ^c	100.0 (9)
Scaly-breasted Thrasher	0 (4)	—
Black-whiskered Vireo	0 (3)	0 (7)
Yellow Warbler	16.7 (6)	14.3 (7)
Adelaide's Warbler	0 (2)	0 (3)
Streaked Saltator ^d	28.6 (7)	—
<i>Loxigilla</i> spp.	0 (8)	0 (2)
Yellow-shouldered Blackbird	—	0 (6)
<i>Quiscalus</i> spp.	63.3 (30)	76.9 (13)

^a Yellow-billed Cuckoo (*C. americanus*) in Puerto Rico and Mangrove Cuckoo (*C. minor*) in St. Lucia.

^b *Progne dominicensis*.

^c Proportions rejecting artificial cowbird eggs were significantly different ($P = 0.00007$; Fisher's exact test).

^d *Saltator albicollis*.

were fledged from Yellow Warbler nests in Puerto Rico than in St. Lucia ($t = 3.6$; $P < 0.001$; Table 2). We detected no interisland difference in the success of cowbird eggs placed in the nest of the other main host, the Black-whiskered Vireo (Table 2).

HOST REPRODUCTIVE SUCCESS

We attempted to determine if brood parasitism affected host reproductive success differently in St. Lucia than in Puerto Rico, by comparing the fates of parasitized and unparasitized nests of two main hosts present in both regions, Black-whiskered Vireos and Yellow Warblers. In St. Lucia, six of 11 (54.5%) unparasitized Yellow Warbler nests fledged at least one young, while three of 16 (18.8%) parasitized nests did so, a significant difference ($P = 0.05$, Fisher's exact test). Mean clutch size and mean number of eggs fledging Yellow Warblers did not differ between parasitized and unparasitized nests.

In contrast to St. Lucia, we detected no difference in the success of Yellow Warbler nests that were or were not parasitized in SW Puerto Rico. However, a higher proportion of parasitized Yellow Warbler nests in Puerto Rico produced host young than nests in St. Lucia (62.5%

of eight nests vs. 18.8% of 16 nests; $P = 0.04$; Fisher's exact test).

Of the 21 parasitized Black-whiskered Vireo nests that we followed in St. Lucia, six (28.6%) produced at least one host fledgling, in comparison to 50% in two unparasitized nests. Three of seven (42.9%) parasitized Black-whiskered Vireo nests in Puerto Rico fledged at least one host young, while three unparasitized nests produced no young. We found no statistical difference on either island between proportions of parasitized and unparasitized vireo nests that produced host young, but sample sizes for unparasitized nests were small. Black-whiskered Vireo clutch size and proportion of host fledglings per parasitized nest were not different between the two islands.

RESPONSE TO ARTIFICIAL COWBIRD EGGS

To examine to what extent observed levels of parasitism may have been affected by hosts' rejection of cowbird eggs, and to determine whether antiparasite behavior differed between regions, we experimentally parasitized 94 nests of 12 species in St. Lucia and 74 nests of 11 species in Puerto Rico (Table 3). In St. Lucia only Gray Kingbirds (*Tyrannus dominicensis*) could be classified as rejecters ($\geq 75\%$ of experimental eggs rejected, Rothstein 1971). All other species tested were accepters. As in St. Lucia, Gray Kingbirds and grackles in Puerto Rico (the Greater Antillean Grackles, *Quiscalus niger*) rejected most experimental eggs, and most other species showed little or no response to experimental parasitism. However, the Tropical Mockingbird (*Mimus gilvus*) in the Lesser Antilles, the Northern Mockingbird (*M. polyglottos*) rejected all the eggs.

DISCUSSION

Any behavior that reduces the impact of brood parasitism should be fixed rapidly (Rothstein 1975). In an area of longer contact with a parasite, hosts would be expected to exhibit defenses such as egg rejection more frequently than in areas contacted more recently. Our data indicated that in St. Lucia only the Gray Kingbird rejected eggs. Rejection behavior was more prevalent in southwestern Puerto Rico, where the cowbird has been in contact with the avifauna for about 40 years less. Furthermore, in both regions, the species that are most often parasitized have the weakest rejection response.

Hosts that have had long periods of contact

with the cowbird may develop adaptations which do not reduce the probability of being parasitized, but which enhance survivability of the nest, once it is parasitized. For example, parental care behavior may change to favor growth of host young (Nakamura, unpubl.). Under such conditions, or under the assumption that other antiparasite behaviors have developed during a period of contact with the cowbird, total reproductive success of parasitized birds in St. Lucia may be expected to be greater than birds in Puerto Rico.

Although the mean number of cowbird eggs in parasitized Yellow Warbler and Black-whiskered Vireo nests did not differ between St. Lucia and Puerto Rico, the number of fledgling cowbirds per warbler nest was higher in Puerto Rico. In St. Lucia parasitized Yellow Warbler nests had lower success than unparasitized nests. At the same time, parasitized Yellow Warbler nests in St. Lucia had lower overall success (proportion of nests producing at least one host young) than those in Puerto Rico. Further, parasitism had no discernible effect on Yellow Warbler productivity in Puerto Rico. Taken together, these results are in the opposite direction of those predicted from a model of host-parasite co-adaptation over time, and suggest that no significant change in antiparasite behavior has occurred during 40 years in St. Lucia.

Although the Shiny Cowbird is not host-specific, in the Caribbean region it has been found to parasitize only a few species (Post and Wiley 1977b, Wiley 1985). Gochfield (1979) discussed host selection according to primary, secondary, and ultimate suitability. Primary suitability relates to distribution in time and space, and accessibility (conspicuousness and degree of nest defense); secondary suitability relates to acceptance; ultimate suitability considers whether, once accepted, the parasite young can survive. In St. Lucia, cowbirds did not parasitize potential hosts according to their abundance. The three most common species in lowland St. Lucia, the Caribbean Elaenia, Carib Grackle, and Adelaide's Warbler, were rarely parasitized. The Carib Grackle is abundant and conspicuous, but its nests may not be accessible because of its colonial nesting behavior and its aggressiveness. Even though we observed a cowbird chick reared to fledging in the nest of a Caribbean Elaenia in St. Lucia, the ultimate suitability of the species may be low, as some portion of its nestling diet is fruit

(Wiley 1988). Adelaide's Warblers may be potential hosts, but nest size may make them primarily unsuitable. Adelaide's Warblers build small nests, which female cowbirds occasionally visit, but do not parasitize (Nakamura, unpubl.).

We examined nests of Gray Kingbirds, Bare-eyed Thrushes (*Turdus nudigenis*), Tropical Mockingbirds, and Scaly-breasted Thrashers (*Margarops fuscus*) in St. Lucia, and found no parasitism. In Puerto Rico nests of the Red-legged Thrush (*Turdus plumbeus*), the Northern Mockingbird, and the Pearly-eyed Thrasher (*Margarops fuscatus*) are rarely or never parasitized (Wiley 1985, this study). Other relatively common, but smaller species were not parasitized on either island: Black-faced Grassquit (*Tiaris bicolor*), Lesser Antillean (*Loxigilla noctis*) (*L. portoricensis*) and Puerto Rican bullfinches, and Bananaquit (*Coereba flaveola*). These species may have low ultimate suitability, as they feed their young with nectar, fruit, and seeds (Wiley 1988, pers. observ.).

What effect is the Shiny Cowbird having on bird populations in St. Lucia? Our study shows that only the Black-whiskered Vireos and Yellow Warblers are regularly and successfully parasitized in lowland areas. Parasitized Yellow Warbler nests fledged fewer young per nest compared to unparasitized nests. Our sample size for unparasitized Black-whiskered Vireo nests was too small to determine whether brood parasitism had any effect. Although we have no direct information on parasitism rates of the St. Lucia Oriole (*Icterus laudabilis*), we made three independent observations of adult orioles feeding young cowbirds, but no oriole young. St. Lucia Orioles were uncommon in our study areas (4.9 individuals/km²), and were encountered at about the same rate, 0.6 individuals/hr, as Diamond (1973) reported 12 years earlier. We found the same densities for the St. Lucia Oriole and the Martinique Oriole (*I. bonana*), which is now regarded as threatened (Johnson 1988), possibly as a result of parasitism by the cowbird (Wood 1987). In the Greater Antilles, the Black-cowled Oriole (*I. dominicensis*) and Troupial (*I. icterus*) are frequently parasitized by Shiny Cowbirds (Wiley 1985, Perez-Rivera 1986, Cruz and Wiley 1989), and it is probable that most species of *Icterus* in the Antilles are affected by cowbird parasitism.

The Shiny Cowbird has the attributes of a good colonizer (Ricklefs and Cox 1972), as it: (1) occupies lowland, open areas; (2) travels in groups;

(3) wanders during the nonbreeding season; and (4) is locally abundant. The species arrived in St. Lucia by 1931, and was in Martinique by 1948 (Post and Wiley 1977a). However, it is not known to have become established on the islands between Martinique and Vieques, a distance of 560 km. Several intervening islands, Guadeloupe and Dominica, are larger than St. Lucia, where the species is now widespread and relatively common. The species is not common on Martinique, and it occurs mainly on the southern end of the island, although suitable hosts are about as common as in St. Lucia. As suitable hosts like Black-whiskered Vireos and Yellow Warblers also occupy islands farther north (Bond 1956), it is possible that the scarcity or absence of the cowbird on these islands is related to ecological requirements which have not been identified.

The Shiny Cowbird is a habitat generalist, but occurs most often in open, patchy areas (Ricklefs and Cox 1972, Post and Wiley 1977a, Cavalcanti and Pimentel 1988). Its successful range expansion is correlated with modification of habitat for agriculture (Post and Wiley 1977a). The association of Shiny Cowbirds with animal husbandry in St. Lucia and other areas suggests that its success in the Antilles is dependent on agriculture that provides food for adult cowbirds. The abundance of cowbirds in Puerto Rico may be related to conversion of coastal grasslands to grain crops like millet, milo, and rice in the 1950s. Similar events have caused an increase in Brown-headed Cowbirds (*Molothrus ater*) in eastern North America (Brittingham and Temple 1983). Rothstein et al. (1980) suggested that successful colonization of the Sierra Nevada by Brown-headed Cowbirds depended on the establishment of feedlots (horse corrals) in an area that has prime host suitability but marginal food availability.

The destruction of forests in St. Lucia for charcoal production may have reduced host availability in lowland areas. Host availability, combined with lack of grain-based agriculture, has probably limited the success of the cowbird in the Lesser Antilles. It is possible that establishment of cowbirds on both St. Lucia and Martinique is influenced by food provisioning to domestic stock. The relative scarcity of Shiny Cowbirds in Martinique may be related to availability of these artificial food sources. Martinique has been deforested to the same degree as St. Lucia, 75% and 79%, respectively. However,

many foodstuffs, such as pork and fowl are not produced in Martinique, to the extent that they are in St. Lucia (FAO 1975). In comparison to Martinique, St. Lucia has a larger number of farms with feedlots. We suggest that the larger numbers of Shiny Cowbirds on St. Lucia, in comparison to Lesser Antillean islands farther north, is related to differences in agriculture, as much as to host availability.

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