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YELLOW WARBLER (*DENDROICA PETECHIA*) BREEDING SUCCESS IN RELATION TO SHINY COWBIRD (*MOLOTHRUS BONARIENSIS*) BROOD PARASITISM IN BOQUERÓN, PUERTO RICO

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Resumen. – Éxito de anidaje del Canario de Mangle (*Dendroica petechia*) en relación a defensas contra el parasitismo de camada del Tordo Lustroso (*Molothrus bonariensis*) en Boquerón, Puerto Rico. – Investigamos la biología reproductiva del Canario de Mangle (*Dendroica petechia*) en relación con el parasitismo del Tordo Lustroso (*Molothrus bonariensis*) en Boquerón, Puerto Rico desde 2001–2002 para determinar si han ocurrido cambios en la frecuencia de parasitismo y en la respuesta de aceptación del hospedero luego de 25 años de manejo de tordos en el área. Se observó una reducción en la frecuencia de parasitismo y carga parasítica comparada con datos anteriores. Treinta y cuatro porciento (n = 21) de los nidos fueron exitosos en producir pichones, con juveniles de canario volando de 19 nidos y juveniles de tordo volando de dos nidos. Ningún nido produjo juveniles de canario y de tordo simultáneamente. Cuarenta y tres porciento de los intentos de parasitismo por parte del tordo fueron rechazados por el Canario de Mangle, bien fuese a través de abandono (33%) o de enterramiento de huevos (67%). Estas cifras son considerablemente mayores a los datos reportados previamente. Ningún juvenil de canario voló de nidos en dónde se aceptó el parasitismo, mientras que no hubo diferencias en el promedio de volantones de canario entre los nidos en dónde hubo enterramiento de huevos de tordo y nidos no parasitados. La rápida manifestación de defensas contra el parasitismo en el Canario de Mangle en relación a otros hospederos comunes sugiere que el rechazo ya se encontraba en el repertorio conductual del canario y fue despertado luego de la llegada del Tordo Lustroso a la isla. Un aumento en las respuestas contra el parasitismo en el Canario de Mangle, junto a los efectos del manejo de tordos, ha reducido el éxito de los tordos en nidos de canario y aumentado la productividad del canario al compararse con datos preliminares.

Abstract. – We studied the reproductive biology of the Yellow Warbler (*Dendroica petechia*) in relation to Shiny Cowbird (*Molothrus bonariensis*) brood parasitism in Boquerón, Puerto Rico from 2001–2002 to determine if changes in parasitism frequency and host's acceptance behavior have occurred after 25 years of cowbird management in the area. A reduction in parasitism frequency and parasitic load was observed when compared with previous data. Chicks successfully fledged from 34% of nests (n = 21),

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with warbler young fledging from 19 nests and cowbird young fledging from two nests. There was no nest were warbler and cowbird young fledged simultaneously. Forty-three percent of cowbird parasitic attempts were rejected by Yellow Warblers, either through desertion (33%) or egg burial (67%). These numbers are considerable higher than previously reported data. No warbler fledged from nests in which parasitism was accepted; whereas there were no differences in mean number of warbler fledglings from nests with buried cowbird eggs and non-parasitized nests. The early manifestation of defenses to brood parasitism in the Yellow Warbler in relation to other common hosts suggests rejection was in the behavioral repertoire of the warbler and was reactivated after Shiny Cowbird arrival to the island. An increase in Yellow Warbler responses against parasitism, coupled with the effects of cowbird management have reduced cowbird success at warbler nests and increased warbler productivity when compared with previous data. *Accepted 2 September 2009.*

Key words: *Dendroica petechia, Molothrus bonariensis,* Yellow Warbler, Shiny Cowbird, brood parasitism, anti-parasite strategies, Puerto Rico.

INTRODUCTION

The range expansion of the Shiny Cowbird (= SHCO, *Molothrus bonariensis*), a brood parasite originally restricted to South America, has been related to a decline of naïve Caribbean bird populations (Post & Wiley 1977a; Cruz *et al.* 1985). Cowbird parasitism depress hosts nest success and productivity by egg removal, decreasing hatching success, nestmate competition, and clutches lost to nest desertion or egg burial (Wiley 1985, Massoni & Reboreda 2002). After successfully colonizing the Lesser Antilles, the SHCO was first observed in the eastern coast of Puerto Rico, in 1955 (Grayce 1957), although it could have arrived a decade earlier to the island (Post & Wiley 1977a). By 1969, it was reported at Guánica State Forest, in the south of the island (Kepler & Kepler 1970). The endemic Yellow-shouldered Blackbird (= YSBL, *Agelaius xanthomus*) was first reported as SHCO's main host (Post & Wiley 1977b), but as the cowbird population increased, other species were found to be highly parasitized (80–90% of nests) as well (Wiley 1985; Pérez-Rivera 1986). From 1975 to 1982, YSBL numbers in Boquerón State Forest (henceforth Boquerón) declined from 1663 to 266 individuals due to cowbird parasitism (Post & Wiley 1977a, Wiley *et al.* 1991; Cruz *et al.* 2005). A management program was initiated in 1975 to protect YSBL's major population from imminent extinction, with the establishment of artificial nesting structures to facilitate the extraction of cowbird eggs and minimize predation, and measures to control the cowbird population size (Wiley *et al.* 1991).

As a result of management practices in Boquerón, YSBL numbers have currently increased near to 800 individuals (Cruz *et al.* 2005). Similarly, parasitism of YSBL nests decreased to 2.7% compared to 67% in non-managed areas like Guánica (López-Ortiz *et al.* 2006). While management is expected to benefit the avian community in general, little is known about how the nesting success of other host species has changed after 25 years of these practices. Scientists (Cruz *et al.* 1985; Wiley 1988) warned against a shift in host use as YSBL availability decreased, and the continuous capture of hundreds of cowbirds around the management area (Cruz *et al.* 2005) appears to support this belief. One such species may be the Yellow Warbler (YWAR, *Dendroica petechia*), originally reported by Wiley (1985) as being heavily parasitized and considered a high-quality host because of similar feeding habits, egg size, and breeding seasons (Wiley 1988). For instance, Cruz *et al.* (1985) found that parasitism rates at YWAR nests in Boquerón increased over the years (1973–1982) with higher SHCO numbers.

Species traditionally affected by brood parasitism have evolved defenses to prevent or correct parasitic attacks (Briskie *et al.* 1992).

Responses against parasitism include shifts in breeding season, mobbing behavior, warning calls, nest concealment, and nest defenses. High cowbird parasitism pressure promotes the evolution of anti-brood parasite defenses in recently parasitized host species (McLaren & Sealy 2000, Ortega & Ortega 2000). According to Rothstein (1975), newly parasitized populations require 20–100 years to change from 80% acceptance to 80% rejection of cowbird eggs. Once rejection appears in the population, it would spread rapidly and it is expected be maintained as long as parasitism-related costs continue to favor this behavior (Cruz & Wiley 1989).

North American YWARs, historically parasitized by the Brown-headed Cowbird (*Molothrus ater*), show nest desertion and egg burial as anti-parasitic behaviors (Briskey *et al.* 1992, Sealy 1995). Cruz *et al.* (1985) did not find any rejection to artificial parasitism from 1973–1982 in a heavily parasitized YWAR population in eastern Puerto Rico. However, Wiley (1982) observed a low incidence of egg burial at naturally parasitized YWAR nests (3%), but this was interpreted as a consequence of cowbird parasitism at unfinished nests. He also found the YWAR to be the most tolerant host to cowbird intrusions. Post *et al.* (1990) found 14% of rejection of artificially parasitized YWAR nests in Puerto Rico from 1982–1987, but classified the species as an acceptor of natural parasitism. In contrast, the Gray Kingbird (*Tyrannus dominicensis*) and the Greater Antillean Grackle (*Quiscalus niger*) were classified as rejecters due to their general aggressiveness and territoriality, which conferred a pre-adaptive value to prevent cowbird parasitism (Wiley 1988).

The main goal of this work was to evaluate the effects of SHCO parasitism on the YWAR's reproductive success in Boquerón, Puerto Rico, where cowbirds have been controlled for 25 years as part of the YSBL management program. Specific objectives were to: (1) study YWAR's nesting success in the area, (2) compare current parasitism frequency with the baseline study of Wiley (1985) to determine if the cowbird management program is currently benefiting the YWAR's nesting success, and (3) determine if the incidence of responses to parasitism have changed in the YWAR after 50–60 years of SHCO presence in the island.

METHODS

Study area. The study was conducted in the Pitahaya section of Boquerón State Forest (17°57'N, 67°08'W; Fig. 1), between the municipalities of Cabo Rojo and Lajas, within a subtropical dry forest (Ewel & Whitmore 1973). The forest lies about 20 km to the west of Guánica, extending along the southwestern coast for 6.5 km and reaching up to 1.2 km inland. It is dominated by a red mangrove (*Rhizophora mangle*) coastal fringe and black mangrove (*Avicennia germinans*) basin forest intermixed with mud flats, salt flats, and ephemeral ponds (García *et al.* 1998). Dry coastal forest, characterized by dry pastures, deciduous trees, and thorny brush, is found along the landward edge of the black mangrove forest. White (*Laguncularia racemosa*) and button (*Conocarpus erectus*) mangroves are also present, but to a lesser extent.

Nest searching and monitoring. Nest searching was conducted from March–July 2001 and 2002 in a 1.48 km^2 area dominated by black mangrove stands and ephemeral ponds. Adult YWAR behavior, such as courtship, territorial defense, and activity of warbler pairs (e.g., adults carrying nesting material), provided clues on nesting activity and stage. Active nests were checked every 2–5 days until chicks fledged or the nest failed. Signs of predation, parasitism, or nest abandonment were noted, and causes of nest failure were determined when possible. The dates marking the initia-

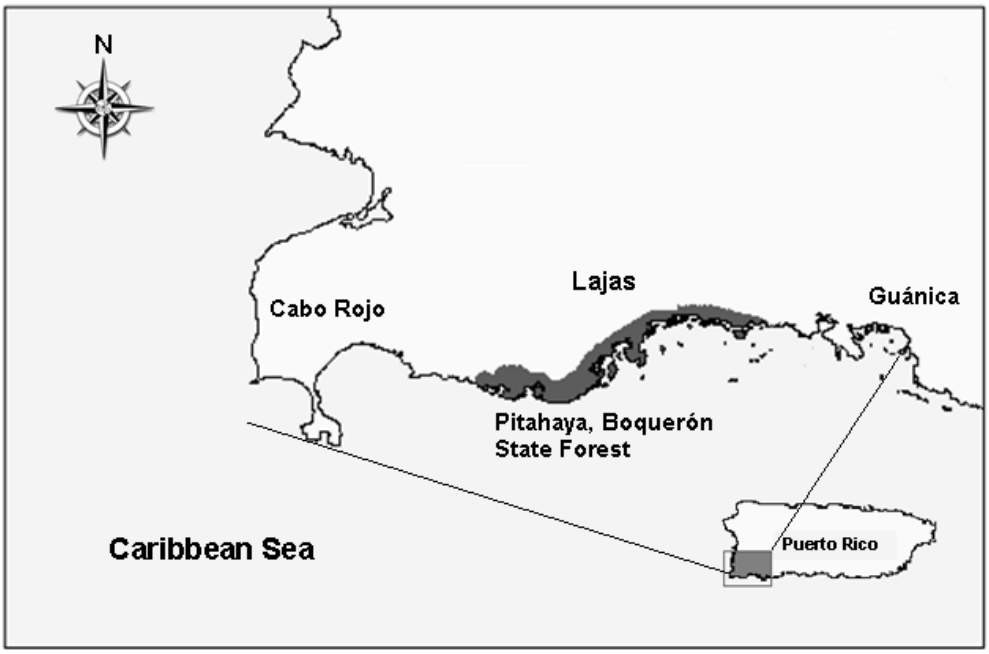

FIG. 1. Map of southwestern Puerto Rico indicating the area of study at the Pitahaya section of the Boquerón State Forest.

tion or end of each stage were assigned by direct observation or by back- or forward-dating from other observed events. YWARs lay three eggs on consecutive days until clutch completion, with incubation starting the second day of egg laying (Prather & Cruz 1995, McMaster & Sealy 1998).

Nest success. A nest was considered successful if either YWAR or SHCO chicks fledged from it (Wiley 1985). On several occasions, nest success was confirmed on the visits following fledging by observation of adults and juveniles in the breeding territories. These observations were reliably assigned to a particular nest, since pairs nested at a considerable distance from each other, and were rarely on the same nesting stage simultaneously. A daily survival rate was calculated for two distinct phases (egg laying-incubation and hatching-nestling) using program MAYFIELD (Hines 1982). Exposure was assumed to start with the laying of the first egg, either host or parasite. Standard errors for the entire nesting period were calculated following Johnson (1979).

Brood parasitism. Only nests found in 2002 were collected and examined after the activity in the nest had ceased to confirm the presence of buried cowbird eggs. Thus, parasitism frequency (number of parasitized nests over total nests) and parasitic load (number of SHCO eggs over total nests) were calculated exclusively from the 2002 dataset. Data from both years were used when calculating nest success, warbler survival, and nest fates according to responses to parasitism.

Behavioral responses to parasitism. YWAR's responses after a parasitism event were classified as: (1) acceptance, if egg laying and incu-

bation continued as usual; (2) desertion, if no adult activity was detected in three visits or the nests appeared untidy; and (3) egg burial, if parasite eggs were fully or partially covered with nesting material, and host eggs were laid over them.

Statistical analyses. Differences in clutch size, number of eggs hatched, and number of chicks fledged between parasitized and non-parasitized nests were examined using Mann-Whitney U-tests. Rates of nest, egg, and chick survival between parasitized and non-parasitized nests and egg and chick rates among SHCO and YWAR individuals at parasitized nests were compared using the program CONTRAST (Hines & Sauer 1989). Fisher's exact tests were used to compare the frequency of predation for parasitized and non-parasitized nests by nesting stage and the proportion of parasitized and successful nests observed in this study, with those reported prior to the initiation of the cowbird management program (Wiley 1985). All results are presented as mean (± SD), except for nest survival and parasitism rates (mean ± SE), with the intention of comparing them with previous data (i.e. Wiley 1985). In all tests, the significance level was set at $P < 0.05$.

RESULTS

Nesting biology. We found 62 active nests during the study, 35 in 2001 and 27 in 2002. Thirty-four (55%) of these nests were found before or on the first day of egg laying, 27 (43%) during incubation, and one (2%) during the fledgling stage. All nests were constructed in mature black mangrove trees. Clutch initiation occurred from 24 April to 1 July in 2001 and from 9 May to 24 June in 2002. Nesting activity extended until 23 July in 2001 and 9 July in 2002, respectively.

There was no difference in YWAR clutch size between parasitized (mean = 2.6 ± 0.51 eggs, n = 14) and non-parasitized nests (mean = 2.5 ± 0.71 eggs, n = 48; $U = 322$, $P = 0.80$). YWAR eggs in parasitized nests hatched an average of 1.7 days after eggs in non-parasitized nests, but this was not statistically significant (parasitized nests: mean = 13.5 ± 1.0 days, n = 4; non-parasitized nests: mean = 11.8 ± 0.72 days, n = 12; $U = 5.0$, $P = 0.23$). However, SHCO eggs hatched significantly earlier than YWAR eggs on the same nests (SHCO: mean = 11.0 ± 0.58 days, n = 7 eggs from five parasitized nests; $U = 5.0$, $P = 0.05$, n = 11). Average nestling days for YWAR chicks at non-parasitized nests was 12.7 ± 1.16 (n = 19) and for cowbird chicks 12.8 ± 2.31 days (n = 3).

Brood parasitism. Two parasitized nests were found in 2001 and 12 in 2002. Eleven nests were parasitized once, while the other three nests received two eggs, resulting in a parasitic load of 1.21 ± 0.43 cowbird eggs per nest for both years. We were able to determine parasitism status for 21 of the 2002 nests collected, meaning a parasitism frequency of 57% (± 0.21 CI).

Responses to parasitism. From a sample of 14 parasitized nests in both years, 8 (57%) YWAR pairs accepted parasite eggs, 4 (29%) buried the egg under the nest lining, and 2 (14%) abandoned their nests. YWARs responded to the presence of a parasite egg in the nest according to the number of warbler eggs present at the time of parasitism. The number of warbler eggs present before parasitism was known for 11 of the 14 parasitized nests: 4 received cowbird eggs before any warbler egg was laid, 6 contained at least one warbler egg when parasitized, and 1 was parasitized three days after the entire warbler clutch was lost, presumably to a female cowbird. In all but one nest parasitized before host egg laying, cowbird eggs were buried under new nesting material. In nests parasit-

ized after clutch initiation, four warbler pairs incubated parasite eggs and two deserted parasitized clutches. Parasitism was accepted in a nest that was parasitized after the entire warbler clutch was lost to depredation. Deserted nests contained warbler eggs laid over a partially covered cowbird egg and were unusually thick, suggesting various consecutive episodes of parasitism followed by egg burial. Egg burial accounted for 67% of all rejections, with warbler eggs being occasionally buried along cowbird eggs. In nests with buried cowbird eggs (n = 2) an average of 2.00 ± 1.41 warblers fledged, but in parasitized nests with accepted parasitism (n = 8) no warbler young was successfully raised. In non-parasitized nests (n = 17), an average of 2.29 ± 0.69 warblers fledged.

Nesting success. Forty-eight percent of nests (30/62) survived the incubation stage, while 34% (21/62) survived until fledging of warbler or cowbird young. Of these, warbler young fledged in 19 nests and cowbird young in two nests. We found no nest where warbler and cowbird young fledged simultaneously (Table 1). Thirty-nine percent (61/157) of warbler eggs and 41% (7/17) of cowbird eggs survived until hatching, while 70% (43/61) of warbler and 43% (3/7) cowbird chicks fledged. Twenty-seven percent (43/157) of warbler eggs and 18% (3/17) of cowbird eggs produced fledglings. Significantly fewer SHCO chicks survived until fledging than YWAR chicks ($P = 0.0002$, Fisher's exact test). Sixty-six percent of active nests (n = 41) failed to produce fledglings (Table 1).

The major cause of nest failure was predation, which accounted for 80% (33/41) of nest losses. Seventy percent (23/33) of nest predations occurred during incubation, with a higher proportion of non-parasitized nests being lost during this stage. Conversely, parasitized nests were more often depredated during the nestling stage (Table 2; $P < 0.001$, Fisher's exact test). Seventy-five percent (6/8) of parasitized nests that accepted cowbird eggs were depredated. Out of 46 non-parasitized nests for both years, 17 (37%) had at least one YWAR chick fledged.

Mayfield nest survival for the incubation period was 0.408 ± 0.013 nest-days and 0.613 ± 0.013 nest-days for the nestling period, years combined. The probability of a nest surviving from egg laying to the fledging of the last chick was 0.27 ± 0.027 nest-days. There was no difference in survival for YWAR and SHCO eggs in parasitized nests (Table 3). Fewer YWAR chicks survived daily from parasitized nests than from non-parasitized nests, with about one chick being lost every day (0.509 ± 0.120 chick-days). Overall, YWAR chicks did not survive in parasitized nests, but SHCO chicks also had a lower survival than YWAR chicks in non-parasitized nests.

Post-management tendencies. The number of parasitized nests decreased significantly with the implementation of the management program (Table 4; $P < 0.001$, Fisher's exact test). A reduction in parasitic load and an increase in the number of YWAR chicks fledged from nests were also observed. This, combined with an increase in YWAR rejection, has resulted in fewer SHCO chicks fledging from parasitized nests. Therefore, a lower proportion of successful nests can be attributed to cowbirds fledging from these nests than those observed before the implementation of the management program (Table 4).

DISCUSSION

YWAR's reproductive success was substantially affected by high predation and parasitism rates, with predation accounting for the vast majority of nest losses. Predation was particularly high during 2002. Potential nest predators in the area include black rats (*Rattus rattus*), feral cats (*Felis catus*), Rhesus (*Macaca*

TABLE 1. Mean number of Yellow Warbler and Shiny Cowbird chicks fledged from non-parasitized and parasitized nests, Boquerón, Puerto Rico, 2001–2002. a. At least fourteen active nests suffered a parasitic event. In five of these cases, parasite eggs were buried under nest lining and incubation of host eggs continued as usual. These cases were considered non-parasitized because the clutch being incubated contained no parasite eggs. Only two of these nests were successful (four YWAR chicks fledged).

	Non-parasitized nests[a]			Parasitized nests[a]		
Parameter measured	Mean ± SD	Range	N	Mean ± SD	Range	N
Active nests (no. of chicks)						
YWAR chicks fledged (43)	0.81 ± 1.17	0–3	53	0	0	0
SHCO chicks fledged (2)	-	-	-	0.33 ± 0.71	0–2	9
Successful nests (no. of chicks)						
YWAR chicks fledged (43)	2.26 ± 0.73	1–3	19	0	0	0
SHCO chicks fledged (3)	-	-	-	1.5 ± 0.71	1–2	2

TABLE 2. Nest fates of parasitized and non-parasitized Yellow Warbler nests, Boquerón, Puerto Rico, 2001–2002. Nests in which cowbird eggs were buried and a new clutch was laid were considered non-parasitized. a. Exact day of initiation of incubation was known for twenty nests. Seven nests with unknown chronology that contained eggs in the visit prior nest predation were included in this category, assuming eggs did not hatch before the nest was found predated (interval between visits averaged 1.72 days). b. A nest that contained three unhatched warbler eggs and two cowbird eggs that hatched but were later predated was included in both categories: hatching failure and predation on nestling stage.

	Percent of nests (n) according to parasitism		
Nest fate	Parasitized (10)	Non-parasitized (52)	Combined (62)
Abandoned during incubation	20 (2)	0 (0)	3 (2)
Predation on incubation stage[a]	10 (1)	42 (22)	37 (23)
Predation on nestling stage[b]	40 (4)	11 (6)	16 (10)
Hatching failure[b]	10 (1)	0 (0)	2 (1)
Weather-related loss	0 (0)	2 (1)	2 (1)
Nest mite-related loss	0 (0)	2 (1)	2 (1)
Human-related loss	0 (0)	6 (3)	5 (3)
Successful-fledged warbler	0 (0)	37 (19)	31 (19)
Successful-fledged cowbird	20 (2)	-	3 (2)

mulatta) and Patas (*Erythrocebus patas*) monkeys, Smooth-billed Ani (*Crotophaga ani*), and common anole (*Anolis cristatellus)*, among others. In addition to predation, low success of non-parasitized nests during the present study is consistent with nesting interference by cowbirds, either to force new chances for parasitism (Arcese *et al.* 1996) or as retaliation to parasitism rejecters (Hoover & Robinson 2007). This is suspected since the majority of non-parasitized nest failures occurred during incubation, when a nest loss would be quickly replaced. Evidence suggests that cowbird presence in an area is associated with a reduction in egg survival and hatching success for non-parasitized nests when compared with nests from a cowbird-free area (Massoni & Reboreda 2002). Conversely, most parasitized nests were lost during the nestling stage. This could be explained by the SHCO chicks'

TABLE 3. Overall nest, egg, and chick survival rates from parasitized and non-parasitized Yellow Warbler (YWAR) nests in Boquerón, Puerto Rico, 2001–2002. Survival is expressed in nest-days, egg-days, and chick-days respectively. SHCO = Shiny Cowbird.

Nest stage/species		Nest survival		Egg survival	Chick survival
		Incubation	Nestling stage		
Overall non-parasitized nests		0.4 ± 0.01	0.7 ± 0.01	-	-
Overall parasitized nests		0.5 ± 0.03	0.4 ± 0.05	-	-
	χ^2	4.53	60.52	-	-
	P	0.03	0	-	-
YWAR - non-parasitized nests		-	-	0.3 ± 0.02	0.7 ± 0.01
YWAR - parasitized nests		-	-	0.4 ± 0.02	0.0 ± 0.09
	χ^2	-	-	5.15	59.73
	P	-	-	0.02	0
SHCO - parasitized nests		-	-	0.4 ± 0.02	0.4 ± 0.03
YWAR - parasitized nests		-	-	0.4 ± 0.02	0.0 ± 0.09
	χ^2	-	-	0	16.25
	P	-	-	1	0.0001

intense begging and noisiness, which draws attention of predators to the nests.

An increase in YWAR responses against parasitism, combined with the effects of cowbird management explains the reduction in the number of cowbird chicks fledged, and the corresponding increase in YWAR productivity compared with data from Wiley (1985). The present study shows that parasitism declined at least 24% after the initiation of the cowbird control program in Boquerón. However, the parasitism rate is still high enough (= 50%) to affect a considerable proportion of YWAR nests. These findings are consistent with a decline in cowbird numbers around Boquerón resulting from trapping, but this may not be totally equivalent to a reduction in the intensity at which cowbirds are parasitizing YWAR nests. In fact, López-Ortiz *et al.* (2006) suggest a shift in SHCO's host preference toward the YWAR in the managed area, as cowbird chicks imprint with warblers at the nest. Presumably this tendency may be a consequence of parasite removal from YSBL nests, preventing cowbirds from fledging from YSBL nests and thus influencing cowbird host choice during adulthood.

About six decades after SHCO arrival to Puerto Rico, the expression of responses to counteract parasitism have strengthened in the YWAR. Although the YWAR seems to have presented what might be considered as defenses as early as 1977 (Wiley pers. com.), its low incidence at that time was not enough to consider the species as a rejecter. Yet, since the presence of a cowbird chick at the nest usually resulted in the loss of the entire YWAR clutch, egg rejection behavior has been highly favored. The YWAR in Boquerón demonstrated a high degree of rejection toward parasitism (43% of parasitized nests), with 67% of these being in the form of egg burial. This behavior might be higher than observed, considering that some types of rejection, such as early nest desertions, might have been missed.

Results from this study suggest that the response to parasite eggs in the nest is deter-

TABLE 4. Summary of nest success, productivity and degree of parasitism of Yellow Warblers, Boquerón, Puerto Rico from 2001–2002 compared with data from 1977–1980 (Wiley 1985).

Component	Year	
	2001–2002	1977–1980
Active nests	59	20
Successful nests (%)	21 (36)	9 (45)
Warbler eggs	149	41
Mean warbler clutch size	2.5 ± 0.67	2.1
Warbler eggs hatched (% of eggs)	60 (40)	14 (34)
Warbler chicks fledged (% of eggs)	43 (29)	7 (17)
Warblers fledged/active nest	0.73 ± 1.14	0.4
Warblers fledged/successful nest	2.05 ± 0.97	0.8
Warblers fledged/successful non-parasitized nest	2.26 ± 0.73	2.33
Parasitized nests (% of nests)	14 (24)	16 (80)
Success of parasitized nests	0.29	0.4
Success of non-parasitized nests	0.38	0.8
Cowbird eggs	17	47
Mean cowbird eggs/parasitized nests	1.21 ± 0.43	2.9
Cowbird eggs hatched (% of eggs)	7 (41)	14 (30)
Cowbird chicks fledged (% of eggs)	3 (18)	7 (15)
Cowbirds fledged/active nests	0.05	0.4
Cowbirds fledged/successful nests	0.14	0.8

mined by YWAR investment at the moment of parasitism. This was observed by Wiley (1985), who found nest desertion rates to be inversely related to number of host eggs at the moment of parasitism. He also found nest desertion rates for parasitized YWAR nests at Boquerón to be significantly higher than for non-parasitized nests. In addition, warblers in eastern Puerto Rico did not lay eggs in nests where a SHCO had laid the first egg, such desertion accounting for 65% of nest failures.

The change in the YWAR's behavior toward parasitism from initial tolerance to rejection is a clear response to the intense parasitism suffered by this species since the arrival of cowbirds. The early appearance of responses against parasitism in the YWAR relative to other species is explained by the species' long history of interaction with brood parasites throughout its range. YWARs in the continental Americas are known to express rejection responses to cowbird parasitism. Thus, it is possible that the behavioral responses against parasitism were not expressed in Puerto Rico because no parasite was evoking them, but the capacity to reject parasites was not entirely lost. Rothstein (2001) suggested egg recognition might be retained in a species lineage long after brood parasitism has ceased (c. 300,000 years), allowing for the expression of egg rejection when again exposed to parasitism. Thus, when strong parasitism pressure was experienced by SHCO arrival, YWARs on the island were able to respond more readily than other species classified as accepters.

The YWAR and other species have benefited from the reduction in cowbird numbers through trapping around Boquerón. But since the SHCO is able to adapt to changes in availability and acceptance behavior of hosts, it would be desirable to monitor this and other

native hosts (e.g., Puerto Rican Vireo, *Vireo latimeri*) to engage in proper management actions if needed. Few YWAR nests have been found outside the managed area, and these face higher parasitism rates than those in Boquerón (López-Ortiz *et al.*, 2006; Medina-Miranda 2008). Higher parasitism outside Boquerón might result in the disappearance of the YWAR despite high parasitism rejection at these populations. Therefore, even if Boquerón serves as a good refuge for breeding populations, it would be advisable to extend the SHCO control and capture to other areas. It would also be useful to determine the degree of recognition of YWARs to SHCO eggs, chicks, and adults, as well to investigate if behavioral defenses, such as aggressiveness to adult cowbirds and nest guarding, help nesting pairs in deterring parasitism.

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