

**YELLOW WARBLER (*Dendroica petechia*) BREEDING BIOLOGY AND
PARASITISM BY THE SHINY COWBIRD (*Molothrus bonariensis*) IN
BOQUERÓN, PUERTO RICO**

by

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ABSTRACT

Abstract- Aspects of the breeding biology of the Yellow Warbler (*Dendroica petechia*) and Shiny Cowbird (*Molothrus bonariensis*) parasitism were studied in Boquerón, Puerto Rico from 2001 to 2002. Fifty-seven percent ($n = 12$) of warbler nests were parasitized. Survival of parasitized nests was lower than non-parasitized nests. Thirty-four percent of nests ($n = 21$) survived until fledging of cowbird or warbler chicks, with predation the major cause of nest failure (88%). Nineteen nests fledged warbler young and two nests fledged cowbird young, but no nest fledged warbler and cowbird young simultaneously. The Yellow Warbler presented three responses toward parasitism: acceptance and incubation, egg burial, and nest desertion. No warbler young fledged from nests that accepted parasitism. Nests with buried cowbird eggs fledged an average of 2.00 ± 1.41 warbler chicks. This study shows that the Yellow Warbler in Puerto Rico expressed anti-parasite strategies three decades after first contact with the Shiny Cowbird.

RESUMEN

Resumen- Se estudiaron aspectos de la biología reproductiva del Canario de Mangle (*Dendroica petechia*) y del parasitismo del Tordo Lustroso (*Molothrus bonariensis*) en Boquerón, Puerto Rico, desde 2001 hasta 2002. Cincuenta y siete por ciento ($n = 12$) de los nidos de canario fueron parasitados. La supervivencia de los nidos parasitados fue menor que la de los nidos no parasitados. Treinta y cuatro por ciento ($n = 21$) de los nidos sobrevivió hasta que volaron pichones de tordo o canario, siendo la depredación la principal causa de pérdidas de nidos (88%). Juveniles de canario volaron de 19 nidos y juveniles de tordo volaron de dos nidos, pero de ningún nido volaron juveniles de canario y de tordo simultáneamente. El Canario de Mangle presentó tres respuestas al parasitismo: aceptación e incubación, enterramiento de huevos y abandono del nido. Ningún juvenil de canario voló de nidos que aceptaron el parasitismo. Los nidos con huevos de tordo enterrados volaron un promedio de 2.00 ± 1.41 juveniles de canario. Este estudio muestra que el Canario de Mangle en Puerto Rico expresó estrategias antiparásitas luego de tres décadas del primer contacto con el Tordo Lustroso.

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DEDICATION

I dedicate this work to the memory of Facundo Pacheco Ramírez and Carmen Luisa Torres, to my parents Claudio Vincenty and Carmen T. Pacheco, and my sister Viviana, who have remained unconditionally by my side. My love and gratitude are also to Fernando Escabí Méndez, who always supported me in moments of despair. And above all, this work is especially dedicated to those adorable feet that always look after me.

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INTRODUCTION

The Yellow Warbler (YWAR-*Dendroica petechia*; Parulidae) is one of the most widespread passerine species in the New World. It is distributed from Canada and Alaska to South America, including the West Indies. Despite the abundance and diversity of Caribbean forms, resident races had received little attention when compared to their migrant counterparts. In opposition to numerous studies of wintering YWAR in the West Indies (Eaton 1953; Lack and Lack 1972; Post 1978; Greenberg and Salgado-Ortiz 1994; Greenberg *et al.* 1996), literature of resident races is limited to several brief notes on their distribution and natural history (Pashley 1988a,b; Pashley and Hamilton 1990, Bond 1930) or documents debating the classification of the various subspecies (Klein and Brown 1994; Aldrich 1942). Furthermore, most studies on YWAR breeding biology have been conducted in temperate regions (Briskie 1995; Studd and Robertson 1989; Ortega and Ortega 2000); and in most cases are not completely applicable to the context of insular tropics.

Island bird populations have decreased due to habitat destruction, forest degeneration, and invasion of alien species (Raffaele *et al.* 1998). Generalized forest clearings in the last century enabled the range expansion of the Shiny Cowbird (SHCO-*Molothrus bonariensis minimus*; Icteridae), a brood parasite original from South America, into the Caribbean region. Brood parasitism is the exploitation of an individual's parental drive by other than its offspring (Alcock 2001). Cowbirds deceive other species into fostering their eggs and chicks, thus freeing themselves of the responsibilities and energetic investments associated with parental care. Female cowbirds lay their eggs in the nests of other birds and fly away, occasionally destroying one or more host eggs. In regions where cowbirds occur naturally, hosts have evolved strategies to resist parasitism (Lotem *et al.* 1995). These include nest concealment, egg and chick discrimination, egg rejection, and nest desertion among others (Payne 1977).

Shiny Cowbird expansion has caused the decline of bird populations since its arrival to newly colonized areas, as is the case of two Puerto Rican endemic species; the endangered Yellow-shouldered Blackbird (YSBL-*Agelaius xanthomus*) (Post and Wiley 1977a) and the Puerto Rican Vireo (*Vireo*

latimeri) in Guánica Commonwealth Forest (Woodworth 1997). SHCO impact on island native species stems from the inexperience of new hosts with parasitic interactions, which results in a decrease in their nest success and productivity (Cruz *et al.* 1985; Wiley 1985).

From 1975 to 1981, 85% of YSBL nests were being parasitized (Wiley 1985). YSBL numbers plummeted, until the main population reached a low of 300 individuals in 1982 (USFWS 1996). As a response, in 1980 the United States Fish and Wildlife Service (USFWS) and the Puerto Rico Department of Natural and Environmental Resources (PRDNER) established a cowbird control program, trapping adult cowbirds, around the Boquerón Commonwealth Forest (BCF), during the non-breeding season. Another component of the control program consisted on removal of cowbird eggs and chicks from YSBL nests since 1991 (López-Ortiz *et al.* 2002).

Currently, the YSBL population has slightly recovered, and continues to do so. Parasitism pressure on this species has decreased dramatically and the number of successful nests has increased accordingly (López-Ortiz *et al.* 2002). While capture reduces cowbird numbers around the BCF, the trapping program does not operate during the breeding season to avoid disturbing nesting YSBLs (Cruz *et al.* 2005). SHCOs typically roost associated with YSBLs and Greater Antillean Grackles (*Quiscalus niger*) in offshore cays close to the BCF, and sometimes follow them to feeding or nesting grounds (Post and Wiley 1992, Cruz-Burgos 1999). Consequently, it is possible for gravid females to gain access to the managed area, and since cowbird eggs and chicks have been removed exclusively from YSBL nests, cowbird chicks might still be fledging from other hosts.

Although SHCO does not parasitize hosts according to their abundance (Wiley 1988), it is capable of changing host preferences within a few generations if availability of the main host is reduced (Payne 1977; Wiley 1985). In the early 1980's, the YWAR was reported as one of the major hosts of the SHCO in the BCF along with the YSBL, Puerto Rican Flycatcher (*Myiarchus antillarum*), Black-whiskered Vireo (*Vireo altiloquus*), Puerto Rican Oriole (*Icterus portoricensis*), and Troupial (*Icterus*

icterus) (Wiley 1985; Cruz *et al.*, 1985). Wiley (1988) recommended special attention to an increase in parasitism rates on other preferred species, as YSBL availability decreased.

In this work I intend to study the breeding biology of the YWAR in southwestern Puerto Rico where a cowbird control program has been ongoing for twenty years. My specific objectives are to (1) assess general aspects of the nesting biology of the YWAR, (2) investigate SHCO parasitism on YWAR after the cowbird management program implementation and its influence on the reproductive success of this species, (3) determine if the YWAR has developed anti-parasite strategies after at least three decades of interaction with SHCO, and (4) propose management practices for the conservation of the species.

LITERATURE REVIEW

Focal Species

The YWAR is a common resident of mangrove forests and coastal habitats such as scrub, lowland rivers, and marshes. This species is particularly abundant in the southern part of the island. Adult plumage is bright yellow with a yellow-green to olive back, a spotless face, and a chestnut striped breast. It usually weights 7.4-16 g and measures about 12 cm long (Fig. 1). In females, ventral streaking is little or absent, and immatures are generally dull gray or green with pale abdomen. Pair formation begins in February and breeding extends from March to July. The cup shaped nest, typically containing three eggs, is frequently constructed close to water, using materials such as fine grass, cotton, plant down, feathers, and occasionally horse hair. (Raffaele *et al.* 1998) The Puerto Rican and Virgin Islands race, *D. p. cruciana*, was described by Sundevall in 1870 from a specimen collected in Saint Croix (Pashley 1988a).



Figure 1. Adult male Yellow Warbler (*Dendroica petechia cruciana*) with distinctive breeding plumage. Photo by Tirtsá Porrata-Doria, Guánica Commonwealth Forest, Puerto Rico, 2005.

Brood Parasitism

The practice of laying one's eggs to be tended by other adults has evolved on several instances in the animal kingdom (e.g., insects, fishes), although it has been more widely documented in birds (Cichón 1996). Brood parasitism can be classified as intraspecific or interspecific, facultative or obligated, and specialized or generalized. Interspecific obligate parasitism is represented in the eastern and western hemisphere in the cuckoo (Cuculidae) and cowbird (Icteridae) families, respectively. In the cuckoos, the effects of parasitism are somewhat diluted, as females belonging to different tribes, specialize in parasitizing different species. Each tribe or gent parasitizes only a small portion of the available nests.

Cowbird parasitism, on the other hand, is generalized, relaying on various species to incubate their eggs, although a preferred host is usually parasitized more heavily. Since cowbirds do not specialize on one species, a reduction in main host numbers will not have any stabilizing effect on the parasite population. The SHCO is known to parasitize up to 232 species, and can easily shift host preferences if necessary (Wiley 1988; Post *et al.* 1990).

How this reproductive strategy first appeared in today's brood parasites is still uncertain. Either cowbirds started laying eggs in nests of conspecifics and gradually parasitized other species or they parasitized other species from the very beginning (Lanyon 1992). Some suggest that an ancestral female lost her nest and was forced to lay her eggs somewhere else (Hamilton and Orians 1965). Others argue that probably cowbird ancestors began reutilizing old nests of their species and gradually evolved into laying eggs on nests that were active (Rothstein 1993). The cowbird species more closely related to the ancestral species, the Screaming Cowbird (*M. rufoaxillaris*) lays its eggs exclusively on related Bay-winged Cowbird (*Agelaioides badius*) nests (Mermoz and Fernández 2003). As cowbird species move away from the ancestral lineage, they tend to use more species as hosts (Lanyon 1992; Rothstein *et al.* 2002).

The underlying mechanisms associated with parasitic behavior have been well documented (Payne 1977; Davies and Brooke 1989). Females usually search for nests by quietly observing host

activities, exploring in suitable habitat, or provoking adult defensive responses by intruding into vegetation (Wiley 1988). Cowbirds select potential hosts according to reproductive synchrony, host's egg size, similarity in nestling diet, type of nest (i.e., no cavity nesting species), and host aggressiveness, among others (Wiley 1988). In general, less aggressive species are parasitized more frequently (Davies and Brooke 1989). Since there is no need for parental care, cowbird reproductive strategy is to produce as many eggs as possible. For instance, a Brown-headed Cowbird female is capable of laying up to 40 eggs in a single breeding season (Scott and Ankney 1983).

Brood parasite specializations include short incubation periods, rapid chick growth, and chick aggressiveness against host's nestlings (Payne 1977; McMaster and Sealy 1998). Parasites depress nest success by destruction of host eggs, decrease in hatching success, nestmate competition often causing starvation of host chicks, and clutches lost to nest desertion or egg burial (Massoni and Reboreda 2002). Some authors suggest that parasitism might cause higher predation rates, another cost for the hosts (McLaren and Sealy 2000). Moreover, host chicks that do fledge from parasitized nests have less chances of surviving their first year than chicks fledged from non-parasitized nests, probably due to malnutrition (Payne and Payne 1998). In a study of Brown-headed Cowbird hosts, Rasmussen and Sealy (2006) suggest that adult feeding may be biased in favor of fledged cowbirds, supporting the notion that costs of parasitism extend well after nesting has passed.

Cowbird eggs usually hatch earlier than host eggs because of reduced energy content (Briskey and Sealy 1990; Kattan 1995). In addition, chicks grow faster, beg more intensely, and are more aggressive than their nestmates (Kattan 1996). This, combined with a bigger gape and usually a longer neck, facilitate cowbird chick monopolization of parental care, reducing the chances of survival of other nestlings (Lichtenstein and Sealy 1998).

Species traditionally affected by brood parasitism have evolved defenses to prevent or correct parasitic attacks (Briskey *et al.* 1992). Responses against parasitism include shifts in breeding season,

mobbing behavior, warning calls, nest concealment, and nest defenses. More directly related to brood parasitism is egg or nestling discrimination and parasite removal from the nest (Payne 1977).

Two hypotheses explain the different degrees of rejection observed among host species (Davies and Brooke 1989; Rothstein 1990). The continuing arms race hypothesis argues that differences in rejection represent stages in the evolution of counter adaptations against parasitism, with species presenting more rejection being interacting with the parasite for longer periods (Payne 1977). The evolutionary equilibrium hypothesis suggests that differences are the result of stabilizing selection, with each species evolving different degrees of rejection, according to constraints, such as intra-clutch variation, or parasite and host egg resemblance (Lotem *et al.* 1992 in Krebs and Davies 1993).

If selection pressure is high, species recently parasitized can evolve defensive strategies after a few generations (McLaren and Sealy 2000; Ortega and Ortega 2000). Rothstein (1975) calculated that parasitized populations would require from 20 to 100 years to change from 80% acceptance to 80% rejection of Brown-headed Cowbird eggs. Since anti-parasite defenses are probably genetically determined (Briskie *et al.* 1992), once parasite recognition and rejection appears in the host population, it would spread rapidly, resulting in either rejecter or acceptor host species (Rothstein 1975).

SHCO range expansion into the Caribbean and southern U.S. was facilitated by the fragmentation of forests that formerly limited its range (Post and Wiley 1977a). Lesser Antilles colonization is believed to reflect a natural island hopping process, whereas in the Greater Antilles, a combination of natural expansion and introductions might have occurred (Cruz *et al.* 1989). An escaped bird was collected in Vieques in 1860 (Newton 1860), but apparently the species did not establish successfully at this time. From 1891 to 1959, the SHCO expanded progressively from Grenada (Bond 1963) to Antigua (Pinchon 1963). SHCO was first detected on Barbados in 1916 (Bond 1956), then on St. Lucia in 1931 (Danforth 1935), and on Martinique in 1948 (Pinchon 1963). It reached Hispaniola by 1972 (Dod 1981), Cuba by 1982 (Garrido *in* Guerra and Alcyon 1987), the Florida Keys by 1985 (Smith and Sprunt 1987), continental United States by 1987 (Smith and Sprunt 1987), and Yucatán, Mexico by 1996 (Kluza 1998).

SHCO arrival in Puerto Rico might have occurred a decade earlier than its first record from Las Cabezas de San Juan in 1955 (Grayce 1957). More detections followed: Yabucoa in 1961 (Biaggi 1963), Quebradillas in 1965 (Buckey and Buckley 1970), and Guánica in 1969 (Kepler and Kepler 1970).

As the SHCO expanded throughout the Caribbean region, native species began experiencing the consequences of brood parasitism. Unsuspicious hosts accepted and incubated cowbird eggs at the cost of a reduced reproductive success and productivity (Wiley 1985). Species affected included endemic races of YWAR and House Wren (*Troglodytes aedon*) and the Martinique Oriole (*Icterus bonana*) in Barbados, Grenada and Martinique respectively (Bond 1966, 1971; Wood 1987). Common host groups throughout the Caribbean include *Myiarchus* flycatchers, vireos, blackbirds (*Icterus* and *Agelaius*), and *Dendroica* warblers (Cruz *et al.* 1989).

In Puerto Rico, the YSBL was reported as SHCO exclusive host (Post and Wiley 1977b), but as the cowbird population increased, more hosts, including the YWAR, were added to the list (Perez-Rivera 1986; Wiley 1988). In 1976 the YSBL was included in the federal list of endangered species mainly due to habitat loss and SHCO parasitism (USFWS 1976). By 1980, almost all YSBL nests were being parasitized (Cruz *et al.* 1985; Wiley 1985). A decrease in YSBL population coincided with an increase in SHCO numbers (Post and Wiley 1977a). From 1974-1982 YSBL populations declined by 80% (1974-1975: 1663 individuals; 1981-1982: 266 individuals) while SHCO populations increased by 20% (1974-1975: 4299 individuals; 1981-1982: 6000 individuals) (Post and Wiley 1977b, Wiley *et al.* 1991; Cruz *et al.* 2005).

As a result, in 1980, USFWS and PRDNER initiated a YSBL Recovery Program in Boquerón, to control SHCO numbers and increase YSBL nesting success and survival. Adult cowbirds were trapped, cowbird eggs and chicks were removed from YSBL nests, and predators and nest mites were controlled in artificial nesting structures placed on main breeding areas (López-Ortiz *et al.* 2002). Management practices in Boquerón resulted in an average YSBL annual increase of 14% with an estimated population of 800 individuals; on the other hand, number of captured cowbirds decreased to 533 individuals in 2003

(Cruz *et al.* 2005). From 1996-1999 number of YSBL nests parasitized decreased to 2.7% compared to 67% in non managed areas (López-Ortiz *et al.* 2002).

The YWAR tops the list of species with most Brown-headed Cowbird parasitism records in North America (Friedmann 1963, Lowther 1993). In St. Lucia the YWAR was the second main host of the SHCO after the Black-whiskered Vireo, with 55% of warbler nests parasitized (Post *et al.* 1990). Relative smaller size, overlap of breeding season, and diet compatibility, makes this a suitable host for the SHCO. Cruz *et al.* (1985) classified the YWAR as a high quality acceptor species. They artificially parasitized 20 nests in Puerto Rico between 1975 and 1982 and none presented any rejection toward parasitism, even when parasitism pressure on natural nests was 64%. Eighty-three percent of warbler nests simultaneously inspected in Hispaniola were parasitized. Moreover, use of this host increased over the years with higher SHCO densities in both islands (Cruz *et al.* 1985). In Martinique, the YWAR made up only 18% of the island potential host population, but was the most frequently parasitized species (Post *et al.* 1990). In Barbados, cowbird parasitism caused the YWAR to become endangered (Raffaele *et al.* 1998).

In North America, the YWAR shows some anti-parasitic behavior including nest desertion and egg burial (Briskey 1992) as this species is too small to reject cowbird eggs by puncturing (Sealy 1995). Egg burial has not been reported from any Caribbean YWAR population, but Wiley (1988) reported that from 1975 to 1981 63% of nests in Boquerón were deserted after a cowbird parasitism event.

METHODOLOGY

Study Site

The study was conducted at the Pitahaya mangrove forest which is part of the BCF (17°57'N, 67°08'W). The BCF is segmented into twelve units totaling 1875.7 ha in the municipalities of Mayagüez, Cabo Rojo, and Lajas. Habitat types within the area include offshore cays, mangrove forests, mud flats, scrubland, alluvial valleys, coral reefs, and sea grass beds (PRDNER 1976).

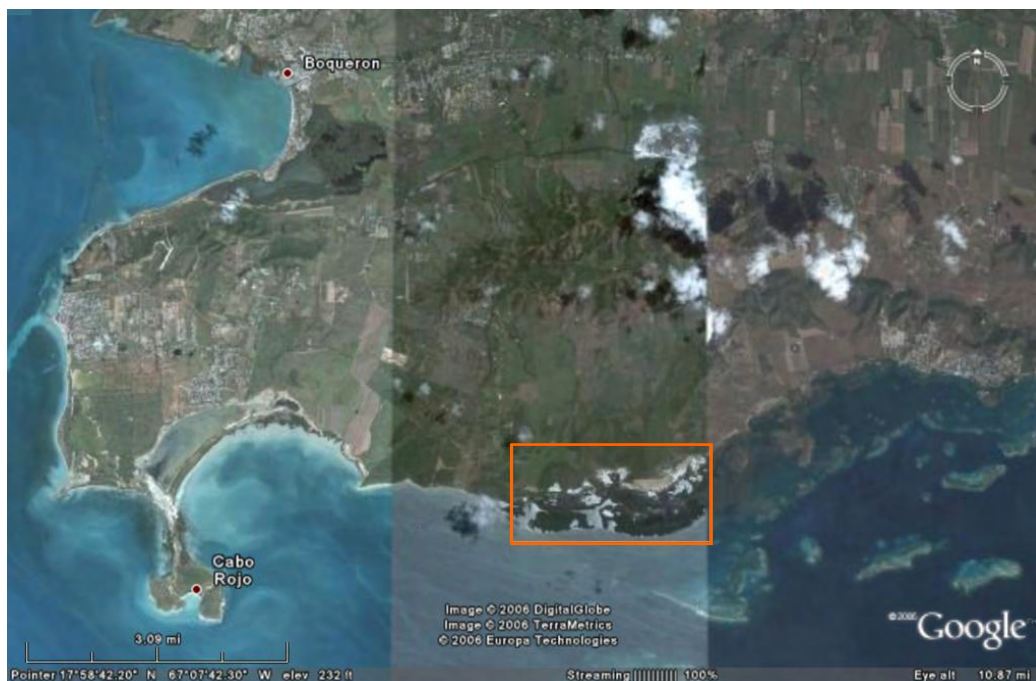


Figure 2. Satellite image of southwestern Puerto Rico indicating area of study at the Pitahaya section of the Boquerón Commonwealth Forest.

The Pitahaya Mangrove Forest runs 6.5 km from Punta Pitahaya to Punta Guayacán connecting with La Parguera, and Bahía Montalva, reaching up to 1.2 km inland (Fig. 2). This tideland is characterized by a red mangrove (*Rhizophora mangle*) coastal fringe and a black mangrove (*Avicennia germinans*) basin forest intermixed with mud flats, salt flats and ephemeral ponds (García *et al.* 1998). White (*Laguncularia racemosa*) and button (*Conocarpus erectus*) mangroves are also present, but to a lesser extent. About 55% of the area is covered by black mangrove, 25% by red mangrove, and 10% is occupied by tidal ponds (Wiley 1985). Hypersaline ponds flood temporally either by rainfall (May-October) or high tide and nearly dry up during the dry season (November-April).

The area was described as Subtropical Dry Forest Life Zone (Ewel and Whitmore 1973). Mean annual rainfall at the closest weather station in Magueyes Island, Parguera for 2001 and 2002 were 60 mm and 38 mm, respectively. In 2001, precipitation ranged from 6 mm in March to 421 mm in May. In 2002, precipitation ranged from 4 mm in November to 105 mm in April. Mean annual temperature for 2001 was 27.2°C (80.9°F) and 27.6°C (81.7°F) for 2002 (UPRM Climatology Center Data).

Along the landward edge of the black mangrove forest, predominates a dry coastal forest characterized by dry pastures, deciduous trees, and thorny brush. Common tree species include mesquite (*Prosopis juliflora*), lignum vitae (*Guaiacum officinale*), oxhorn bucida (*Bucida buceras*), gumbo-limbo (*Bursera simaruba*), and Jamaica caper (*Capparis cynophallophora*). Button mangrove sometimes grows with dry brush and grasses near ephemeral ponds. Some species of shrubs include wild sage (*Lantana involucrata*), neea (*Neea buxifolia*), and box briar (*Randia aculeata*). Spanish dildo (*Cephalocereus royenii*) is one of the most common cacti on the area (Cruz-Burgos 1999, Wiley 1985).

Nest searching and monitoring

The study was conducted from March to July 2001 and 2002. Nest searching concentrated around ephemeral ponds and mangrove stands at the Pitahaya forest. Six sections were identified as: Pond 1, Pond 2, Pond 3, Post, Isla, and Puente (Fig. 3). I searched for nests walking through the mangroves that surrounded each pond, paying special attention to courtship behavior, territorial defense, and activity of warbler pairs (e.g., adults carrying nesting material). Other cues to find nesting territories were adult responsiveness to the investigator, warning calls, and quiet flushing from the vegetation.

The location of each nest was marked with flagging tape and a GPS reading. Adult behavior near the nest provided clues on nest activity and stage. Nests were examined for number of host and parasite eggs, chicks, and fledglings. Cowbird eggs and chicks were readily identifiable from warbler eggs and chicks by appearance and size. Warbler eggs presented an off-white background with reddish spotting, especially around the broad end. Cowbird eggs had a grayish blue or white background with numerous chocolate and reddish spots (Fig. 4). Eggs and chicks were marked for identification with non-toxic

paint. Egg dimensions were recorded to the nearest 0.1 mm for 15 nests in 2001. Each cowbird heard or seen in the vicinity of the nest was recorded. Nests were checked every 2-5 days until chicks fledged or the nest failed and causes of nest failure were determined when possible.



Figure 3. Satellite image demonstrating main locations examined at the Pitahaya section of the Boquerón Commonwealth Forest. A = Pond 1, B = Pond 2, C = Pond 3, D = Post, E = Isla, and F = Puente.

Nest success estimates

Only active nests were included in the analyses. A nest was considered active when at least one host egg or parasite eggs had been laid and incubated, while it was successful if either YWAR or SHCO chicks fledged (Wiley 1985). On several occasions, nest success was confirmed on the visits following fledgling by observation of adults and juveniles in the breeding territories. A nest was considered deserted if (1) adults were not observed after three visits, (2) eggs were no longer incubated or appeared embedded into the nest lining, or (3) the nest showed no signs of maintenance.

In nests encountered late in the nesting cycle, clutch initiation was estimated counting backward from the day of hatching of the first egg, assuming that eggs are laid on consecutive days and that the incubation period is about 11.9 ± 0.39 days (McMaster and Sealy 1998; Lowther *et al.* 1999). In nests found with chicks, the day of hatching was estimated by counting backward from the day of fledging of

the first chick, assuming eggs hatch on consecutive days and that nestling period is about 12 days (Prather and Cruz 1995). When date of fledging was not available, either because of nest predation or because the nest was not visited afterwards, the size of individual chicks served as cues to estimate nest chronology. Nest chronology could not be determined in nests with unknown nest initiation that disappeared before hatching or fledgling (Mayfield 1975).

Incubation was assumed to start the day before clutch completion (i.e., second day of egg laying). Nestling period was defined as the time elapsed from hatching of the first egg to fledgling of the last chick. In the absence of other cues, any relevant event that occurred between visits (e.g., predation, parasitism) was estimated to occur in the midpoint between these.

A daily survival rate was calculated at nest, egg and nestling levels using the Mayfield estimator of survival (Mayfield 1961, 1975). Mayfield's estimator of daily nest survival counts all nests surviving during a given interval and divides it by the total exposure (nest-days) for all nests during this interval. I subdivided nest history into two distinct phases: egg laying-incubation and hatching-nestling, and determined the number of nests, eggs or chicks surviving in each phase. Since this method is based on intervals between days, it is impossible to calculate survival for one day separately. Consequently, for these calculations only, I assumed incubation started on the first day of egg laying to include nests that were lost before or on the second day of egg laying. Exposure was calculated with the laying of the first egg, either host or parasite. In nests in which cowbird eggs were buried under nest lining, I calculated exposure with the laying of the first warbler egg. Partial or sequential predation of eggs or chicks were ignored. A nest was considered predated only when entire nest contents were lost.

To obtain the survival rate for each phase, the daily survival rate is raised to the number of days this period lasts. The probability of survival for a nest is obtained by multiplying the probability of survival during the incubation period and the probability of survival during the nestling period. This model assumes (1) a constant mortality rate throughout each nesting stage, (2) losses directly proportional

to the exposure, (3) independence of observations (each observation represents a binomial trial), (4) nesting stages have the same duration for all nests. I used Program Mayfield[®] (Hines 1982) to estimate survival rates. This program uses the Bart and Robson (1982) maximum-likelihood estimator for the Mayfield survival rate. Standard errors for the entire nesting period were calculated following Johnson (1979).



Figure 4. Comparison of egg dimensions and appearance between Shiny Cowbird and Yellow Warbler eggs. Cowbird eggs were readily identifiable by their larger size and bluish gray background.

Brood parasitism

A daily parasitism rate was calculated following Pease and Gzybowski (1995) model to estimate seasonal female fecundity. To estimate daily parasitism rate, a window of susceptibility to this event must be defined. A nest is susceptible to parasitism from the day before egg laying to a day after it ceases, assuming all eggs are laid on consecutive days. As YWAR clutches usually contain three eggs, nest vulnerability to parasitism usually spans five days. Daily parasitism rate was obtained by dividing the number of parasitism events during the window of susceptibility by the total days of exposure during the window. In nests with more than one cowbird egg, parasitism events corresponded to the number of

cowbird eggs. Nests active during a portion of the window were included until the last day the nest was observed active or until the end of the window (e.g., when a nest was parasitized and subsequently deserted or predated during susceptibility). But if desertion or predation occurred after the susceptible period had passed, all days in the window were included. Parasitism events outside this window and corresponding days of exposure were not included in calculations. Nests with unknown chronology were excluded from the calculations. Standard errors were calculated assuming binomial trials (Fowler and Cohen 1996).

A seasonal parasitism fraction was calculated by dividing the number of parasitized nests over the total number of nests in the breeding season. Only nests that (1) were found before or on the first day of egg laying, and (2) were active during all the window of susceptibility to parasitism were included (Woodworth 1997). Parasitized nests that met these criteria were included in calculations regardless of warbler anti-parasitic responses (i.e., egg burial, nest desertion). Nests with unknown chronology were excluded from calculations. Daily parasitism rate and seasonal parasitism fraction were calculated from 2002 data only.

When comparing number of chicks fledged from parasitized and unparasitized nests, nests in which cowbird eggs were buried and the YWAR clutch continued as usual, were considered as unparasitized clutches. To calculate parasitism frequency (number of parasitized nests over total nests) and pressure (number of SHCO eggs over total nests), I only included nests in which presence or absence of parasitism was confirmed either by collection or direct observation of nests. Nests were collected in 2002 in search of buried cowbird eggs. I assumed that nests containing two cowbird eggs represented two independent events of parasitism by different females.

Behavioral responses to parasitism

The YWAR is too small to expect egg ejection to be a potential response against parasitism (Rothstein 1975, Clark and Robertson 1981). I classified Yellow Warbler responses after a parasitism event as: (1) acceptance, if egg laying and incubation 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. With nests found late in the nesting cycle, egg burial was confirmed after nesting activity ceased and nests were collected.

Clark and Robertson (1981) and Burgham and Picman (1989) found that YWAR anti-parasitic response could vary according to clutch size prior to parasitism. I tried to determine which responses to parasitism predominated according to stage in the egg laying sequence. For instance, if they deserted nests or buried eggs in a particular stage.

Statistical Analyses

Nest inclusion criteria and sample size varied among different tests. These are specified with each table or analysis. Significance level was set at $\alpha = 0.05$ and all tests performed were two-tailed. Descriptive statistics (e.g., clutch size, incubation period) were presented as mean \pm SD, while other values and estimates (e.g., survival and parasitism rates) were presented as mean \pm SE.

Average clutch size, number of eggs hatched and number of chicks fledged did not vary between years (Mann-Whitney U -tests, $p > 0.05$); consequently, both years were combined. I used Mann-Whitney U -tests to compare clutch size, number of eggs hatched, and number of chicks fledged between non-parasitized nests and parasitized nests with different types of responses toward parasitism and between nests that accepted and rejected parasitism.

I used program CONTRAST (Hines and Sauer 1989) to compare nest, egg, and chick survival rates between parasitized and non-parasitized nests and between SHCO and YWAR individuals at parasitized nests. This program performs a Chi square test equivalent to the Brownie *et al.* (1985) z -test for two groups; for more than two groups the program computes a Chi square quadratic form test.

Frequency of predation for parasitized and non-parasitized nests by nesting stage was analyzed with Fisher's exact tests. This test was also used to compare proportion of parasitized nests, and successful nests observed in this study with those observed prior initiation of the management program.

RESULTS

Breeding Biology

A total of 62 active nests was found during the course of 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 on mature black mangrove trees along or in the vicinity of ephemeral ponds.

Clutch initiation occurred from 24 April to 1 July 2001 and 9 May to 24 June 2002, peaking around late May and mid-June 2001 and 2002. Nesting activity continued until July 23, 2001 and July 9, 2002, with higher number of active nests during early May and mid-June, 2001 and late May and June, 2002. Maximum number of eggs was observed during late April and mid June, 2001 ($n = 55$) and mid-May and mid-June, 2002 ($n = 40$). A maximum number of chicks was observed during late June, 2001 ($n = 24$) and 2002 ($n = 16$).

Average clutch size for both years, including parasitized nests was 2.5 ± 0.67 eggs ($n = 62$). Average clutch size excluding parasitized nests was 2.5 ± 0.71 ($n = 48$); clutch size for parasitized nests was 2.6 ± 0.51 ($n = 14$). There was no difference in clutch size between parasitized and non-parasitized nests ($U = 322$; $p = 0.80$, $n = 62$; Mann-Whitney U-test). Average egg dimensions were as follows: YWAR ($n = 31$), 17.7 ± 0.8 mm (length) per 13.3 ± 0.6 mm (width); SHCO ($n = 5$), 21.2 ± 0.9 (length) per 16.1 ± 0.5 mm (width).

YWAR incubation period for 12 non-parasitized nests found before egg laying and surviving until hatching was 11.8 ± 0.72 days. For parasitized nests, mean number of days until hatching of the first YWAR egg was 13.5 ± 1.0 days ($n = 4$). This represents an increase of 1.7 days when compared with non-parasitized nests, but this difference was not statistically significant ($U = 5.0$; $p = 0.23$, $n = 16$; Mann-Whitney U-test).

I calculated days to hatch for cowbird eggs from five parasitized nests that survived until hatching of the first parasite egg. I assumed females could recognize their own eggs and the presence of a foreign egg did not elicit an earlier incubation (i.e., incubation started with the laying of the second warbler egg). Shiny Cowbird eggs hatched after 11.0 ± 0.58 days ($n = 7$ eggs). Shiny Cowbird eggs hatched earlier than YWAR eggs on the same nests ($U = 5.0$; $p = 0.05$, $n = 11$; Mann-Whitney U-test).

Nestling stage was assumed to extend from the hatching of the first egg until the fledging of the last chick. Average nestling days for the YWAR was calculated from 19 non-parasitized nests from both years with complete records from hatching to fledging of chicks ($\bar{x} = 12.7 \pm 1.16$ days). On average, cowbird chicks fledged after 12.8 ± 2.31 days ($n = 3$).

Brood parasitism

Seventeen events of parasitism were observed in 14 active nests during the study. Proportion of active nests parasitized was 6% for 2001 ($n = 2$) and 44% for 2002 ($n = 12$). Eleven nests were parasitized once, while other three nests received two eggs, with an average of 1.21 ± 0.43 cowbird eggs per nest for both years. Since nests were not collected in the first year and I did not count buried eggs, I calculated parasitism frequency and pressure from 2002 nests only ($n = 27$). I was able to assign a parasitism condition with certainty for 21 of these nests with 57% of them being parasitized (± 0.21 CI). In addition, these nests received 14 cowbirds eggs, for a parasitism pressure of 67% (± 0.21 CI). A seasonal parasitism fraction was calculated as well for 10 nests that met the criteria listed in the section of methodology. Estimated seasonal parasitism fraction for 2002 was 0.5 ± 0.17 .

The daily parasitism rate was calculated from four parasitized nests with a total of five cowbird eggs and 35 days of exposure. Five nests parasitized outside the window of susceptibility to parasitism and tree nests with unknown chronology were excluded from calculations. Female cowbirds parasitized susceptible nests at an estimated rate of 0.14 ± 0.06 cowbird eggs per day. The window of susceptibility to parasitism contained 40% of all cowbird egg laying events observed. All nests parasitized inside this window accepted parasitism, whereas all nests parasitized before this window were buried ($n = 4$). One

nest parasitized after the window, was accepted, even though parasitism occurred three days after the entire YWAR clutch was lost.

Based on this information, and assuming all nests start on the same day and that a nest will be parasitized only once by the same female, one could expect that after five days of susceptibility about 53% of nests will receive a cowbird egg. Since parasitism events inside this window only represent 40% of all parasitism events, a total 132.5 cowbird eggs will be laid per 100 parasitized nests. This estimate of 1.32 ± 0.125 cowbird eggs per parasitized nest is not different from the observed value of 1.21 ± 0.43 cowbird eggs per nest for both years ($p = 0.33$; two-tailed significance of χ test).

Table 1. Number of parasitized Yellow Warbler nests and type of response depending on clutch size at moment of parasitism, Boquerón, Puerto Rico, 2001-2002.

Yellow Warbler eggs at the moment of parasitism ^a	Type of Yellow Warbler response to parasitism event		
	Nests with Incubation	Nests with Egg Burial	Nests with Abandonment
0	2 ^b	3	-
1	3	-	2 ^d
2	1	-	-
Unknown	2	1 ^c	-

a No information on response with three warbler eggs because of small sample size.

b In one of these nests parasitism was accepted after loss of entire clutch.

c Nest found with two warbler eggs laid over two buried cowbird eggs. It could have been parasitized with zero warbler eggs or with one warbler egg that was removed by the female cowbird.

d Both nests apparently suffered successive parasitic and burial events. Cowbird eggs were partially buried before desertion.

Three responses toward the presence of a parasite egg in the nest were observed: (1) acceptance and incubation of the cowbird egg, (2) burial of cowbird eggs -occasionally with warbler eggs- under nesting material, and (3) nest desertion. Out of 14 parasitized nests, 8 (57%) accepted parasite egg(s), 4 (29%) buried the egg under nest lining and 2 (14%) were abandoned. When only 2002 data are included a 1:1 ratio of acceptance and rejection is observed ($n = 12$).

Both nests deserted in 2002 were suspected to have been parasitized previously and to have buried cowbird, and possibly warbler eggs, under the nesting material. These nests were unusually thick, suggesting that they were successively parasitized after burial of the first cowbird egg, but it could not be

confirmed because they were predated before they could be collected. Table 1 shows type of anti-parasitic response in relation to the number of YWAR eggs in the nest before parasitism. Typically, acceptance occurred when warbler eggs were present in the nest at the moment of parasitism. In addition, all but one nest in which egg burial was evidenced had only cowbird eggs buried ($n = 5$), and in the remaining nest only one warbler egg was buried with the cowbird egg. Moreover, I did not observe any nest desertion before or during the egg laying stage (Table 2).

Table 2. Nest fates of parasitized and non-parasitized Yellow Warbler nests, Boquerón, Puerto Rico, 2001-2002.

Nest fate	Percent of nests (n) according to parasitism ^a		
	Parasitized (10)	Non-parasitized (52)	Combined (62)
Abandoned ^b during egg laying	0	0 (0)	0 (0)
Abandoned ^b during incubation	20 (2)	0 (0)	3 (2)
Predation on incubation stage ^c	10 (1)	42 (22)	37 (23)
Predation on nestling stage ^d	40 (4)	11 (6)	16 (10)
Hatching failure ^d	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)

a Five parasitized nests that buried cowbird eggs were considered as non-parasitized clutches.

b Two nests were found containing warbler eggs and one cowbird egg partially covered in nest lining. Nests were unusually high and were suspected to contain a cowbird egg buried from a previous parasitic event. Apparently after a second parasitic event, adults started a new nest layer, but then abandoned the nests.

c 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).

d One nest contained three warbler and two cowbird eggs. Warbler eggs never hatched, but cowbird eggs did. The nest was later predated with two cowbird chicks. This nest was included in both categories: hatching failure and predation on nestling stage.

Reproductive Success

Thirty nests (48%) survived incubation stage and 21 (34%) survived until fledging of warbler or cowbird young. Nineteen nests fledged warbler young and two nests fledged cowbird young. No nest fledged warbler and cowbird young simultaneously. 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) cowbird eggs produced young. Significantly fewer SHCO chicks survived to fledge than YWAR chicks ($p= 0.0002$ Fisher's exact test).

Sixty-six percent of active nests ($n = 41$) were lost. The major cause of nest failure was predation with 80% ($n = 33$) of nests loses. In addition, one nest failed because of nest-mite infestation, one was affected by heavy rainfall and three nests were suspected to fail because of human disturbance. Twenty-three (81%) of all nest predations occurred during incubation and 10 (30%) during the nestling stage (Table 2). Eggs in some of the nests that failed ($n = 4$) were observed sequentially predated over a period of 2-3 consecutive days. On several occasions ($n = 4$), nest were partially predated, but the nest continued until hatching of the remaining eggs.

Parasitism was suspected to be related to some nest and egg losses. In 2002, two nests were abandoned after parasitism, and were later predated upon. In one occasion, a female cowbird was observed at a distance of 5 m from an inactive nest (visit 2), on visit 4 the nest showed evidence of predation and on visit 6 a single cowbird egg was being incubated (four days elapsed between visit 3 and 4). This nest was later predated. Removal of warbler eggs by cowbirds was also suspected for other nests ($n = 4$).

Table 3. Mean number of Yellow Warbler and Shiny Cowbird chicks fledged from non-parasitized and parasitized nests, Boquerón, Puerto Rico, 2001-2002.

Parameter measured	Non-parasitized nests ^a			Parasitized nests ^a		
	Mean \pm SD	Range	<i>n</i>	Mean \pm SD	Range	<i>n</i>
Active nests (No. of chicks)						
YWAR chicks fledged (43)	0.81 \pm 1.17	0-3	53	0	0	0
SHCO chicks fledged (2)	-	-	-	0.33 \pm 0.71	0-2	9
Successful nests (No. of chicks)						
YWAR chicks fledged (43)	2.26 \pm 0.73	1-3	19	0	0	0
SHCO chicks fledged (3)	-	-	-	1.5 \pm 0.71	1-2	2

a. A nest was considered successful when at least one SHCO or YWAR chick fledged. 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 five cases were included as non-parasitized because the clutch being incubated contained no parasite eggs. Two of these nests incubated 3 YWAR eggs, and three incubated 2 YWAR eggs with one of these burying one YWAR egg with the cowbird egg. Only two of these nests were successful (4 YWAR chicks fledged).

Although nests that fledged only SHCO chicks were considered successful, net reproductive gain for the YWAR is null, so these might be considered nest failures as well. It is also interesting to note that all but two of the parasitized nests that accepted parasitism ($n = 8$) were predated. A higher proportion of non-parasitized nests was predated on the incubation stage, whereas parasitized nests were more often predated during the nestling stage (Table 2; $p = 0.00$ Fisher's exact test).

Out of 46 non-parasitized nests for both years, 17 (37%) fledged at least one YWAR chick. Also, two parasitized nests that buried the parasite eggs fledged warbler young successfully, but none of the eight parasitized nests that accepted parasitism fledged warbler young (years combined). Successful non-parasitized clutches fledged an average of 2.26 ± 0.73 warbler chicks (Table 3). YWAR chicks ($n = 8$) were observed in only four parasitized nests, and these survived for no more than two days. Forty-four percent (4/9) nests that accepted parasitism survived until hatching of YWAR eggs. Eggs in the remaining nests were predated or did not hatch. Apparently, YWAR chicks died of starvation, being unable to compete with their parasite nestmates.

Table 4 compares nest success and breeding biology parameters of 2001 and 2002 with data from 1977-1980 (Wiley 1985). Percent of parasitized nests has decreased significantly after the management program ($p = 0.00$ Fisher's exact test). Also, there is a tendency of fewer SHCO eggs per parasitized nest and an increase in YWAR chicks fledged from nests. A reduction in SHCO chicks fledged per nests is also observed, presumably as a result of YWAR rejection of parasitism. Since a nest was considered successful when any kind of chick fledged, the lower proportion of successful nests after the management program (36% vs. 45%) is explained by a reduction in number of nests that are fledging cowbird chicks. This is observed comparing mean number of warblers fledged per successful nests before and after the program (0.8 vs. 2.5) with mean number of cowbirds fledged per successful nests (0.8 vs. 0.14) before and after the program.

Table 4. Summary of nest success, productivity and degree of parasitism of Yellow Warblers, Boquerón, Puerto Rico, 2001-2002; 1977-1980.

Component	Year			
	2001	2002	Combined	1977-1980 ^a
Active nests	32	27	59	20
Successful nests (%)	14 (44)	7(26)	21 (36)	9 (45)
Warbler eggs	85	64	149	41
Mean warbler clutch size	2.7 ± 0.60	2.4 ± 0.63	2.5 ± 0.67	2.1
Warbler eggs hatched (% of eggs)	34 (40)	26 (42)	60 (40)	14 (34)
Warbler chicks fledged (% of eggs)	27 (32)	16 (26)	43 (29)	7 (17)
Warblers fledged/ active nest	0.84 ± 1.17	0.59 ± 1.12	0.73 ± 1.14	0.4
Warblers fledged/ successful nest	1.93 ± 1.00	2.29 ± 0.95	2.05 ± 0.97	0.8
Warblers fledged/ succ. non-paras. nest	2.25 ± 0.62	2.29 ± 0.95	2.26 ± 0.73	2.33
Parasitized nests (% of nests)	2 (6)	12 (44)	14 (24)	16 (80)
Success of parasitized nests	1.00	0.17	0.29	0.4
Success of non-parasitized nests	0.40	0.33	0.38	0.8
Cowbird eggs	3	14	17	47
Mean cowbird eggs/ parasitized nests	1.5 ± 0.71	1.17 ± 0.39	1.21 ± 0.43	2.9
Cowbird eggs hatched (% of eggs)	3 (100)	4 (29)	7 (41)	14 (30)
Cowbird chicks fledged (% of eggs)	3 (100)	0 (0)	3 (18)	7 (15)
Cowbirds fledged/ active nests	0.09	0	0.05	0.4
Cowbirds fledged/successful nests	0.21	0	0.14	0.8

^a Wiley 1985.

When comparing clutch size, number of eggs hatched or number of chicks fledged between non-parasitized nests and parasitized nests according to each response to parasitism, significant differences were found in number of chicks fledged from non-parasitized nests and nests that accepted parasitism ($U = 112$; $p = 0.04$, $n = 53$; Mann-Whitney U-test) and between nests that buried cowbird eggs and nests that accepted parasitism (Table 5; $U = 8$; $p = 0.05$, $n = 12$; Mann-Whitney U-test).

Table 5. Mean clutch size, number of eggs hatched, and number of chicks fledged in non-parasitized and parasitized Yellow Warbler nests, Boquerón, Puerto Rico, 2001-2002.

Variable	Non-parasitized	Parasitized nests		
	Nests	Acceptance	Burial	Desertion
Clutch size	2.44 ± 0.73	2.75 ± 0.46	2.50 ± 0.58	2.00 ± 0.00
<i>n</i>	48	8	4	2
YWAR eggs hatched	2.24 ± 0.70	1.75 ± 0.50	2.33 ± 1.15***	0.00 ± 0.00***
<i>n</i>	21	4	3	0
YWAR chicks fledged	2.29 ± 0.69***	0.00 ± 0.00***	2.00 ± 1.41***	0.00 ± 0.00***
<i>n</i>	17	0	2	0

Table 6 shows daily survival rates for all nests (parasitized and non-parasitized). Mayfield nest survival for the entire incubation period was 0.408 ± 0.013 nest-days and 0.613 ± 0.013 nest-days for the entire nestling period, years combined. The probability of a nest surviving from egg laying to the fledging of the last chick was calculated as 0.27 ± 0.027 nest-days. Nest survival over the entire nesting history was significantly lower in 2002 ($X^2 = 21.3$; $df = 1$, $p = 0.00$).

Table 6. Daily and overall nest survival rates of Yellow Warbler nests in Boquerón, Puerto Rico, 2001-2002.

Year	No. nests	No. obs. Days	Mean (\pm SE) nest survival rate		
			Daily survival rate by nest stage		Overall survival rate
			Egg laying and incubation	Nestling	Egg laying through nestling ^a
2001	32	272	0.926 ± 0.017	0.993 ± 0.007	0.363 ± 0.00
2002	26	203	0.932 ± 0.018	0.923 ± 0.030	0.152 ± 0.039
Combined	58	475	0.928 ± 0.013	0.969 ± 0.012	0.271 ± 0.027

^a For overall survival rate calculations I assumed egg laying-incubation and nestling stages spanned 12 and 13 days respectively.

Table 7 details Mayfield estimates of nest survival for parasitized and non-parasitized nests during incubation, nestling, and for the whole nesting history. Daily survival rates did not differ significantly between parasitized and non-parasitized nests during incubation or nestling, except for 2001. This difference arises from small sample size for parasitized nests in 2001 ($n = 2$). Survival of parasitized nests over the entire nesting history was significantly lower than non-parasitized nests when years were combined ($X^2 = 26.7$; $df = 1$, $p = 0.000$).

YWAR eggs from parasitized nests lasted as long as SHCO eggs in those same nests. This means that egg survival of YWAR and SHCO were only subject to predation and there was no difference in survival between them (Table 8). On the other hand, fewer YWAR chicks survived daily from parasitized nests than non-parasitized nests ($X^2 = 14.9$; $df = 1$, $p = 0.0001$), with about 50% of them being lost everyday. Overall survival of YWAR chicks in parasitized nests is null, but survival of SHCO chicks was greatly reduced when compared with YWAR survival from non-parasitized nests (Table 9).

Since in 2001 all SHCO chicks ($n = 3$) observed survived (survival = 1.00) and in 2002 all four SHCO chicks ($n = 4$) observed died (survival = 0) a reliable estimate of SHCO chick survival could not be obtained from this study. However, it appears from this data that SHCO are not being very successful in producing young (at least at YWAR nests in BCF). A combination of factors for this may include the management program which reduces adult numbers in Boquerón, YWAR defensive strategies toward parasitism and more intense predation on parasitized nests.

Table 7. Daily and overall nest survival rates of parasitized and non-parasitized nests of Yellow Warbler in Boquerón, Puerto Rico, 2001-2002. Survival is expressed in nest-days.

Mean (\pm SE) nest survival rate				
Incubation Stage				
Year	Daily Survival Rate		Survival for Entire Period	
	Non-parasitized nests	Parasitized nests	Non-parasitized nests	Parasitized nests
2001	0.917 \pm 0.019 ***	1.000 \pm 0.000 ***	0.353 \pm 0.016 ***	1.000 \pm 0.000 ***
<i>n</i>	30	2	30	2
Exposure	244	26	244	26
2002	0.942 \pm 0.021	0.916 \pm 0.033	0.488 \pm 0.021	0.348 \pm 0.405
<i>n</i>	17	9	17	9
Exposure	121	69	121	69
Combined	0.926 \pm 0.014	0.937 \pm 0.025	0.398 \pm 0.013 *	0.458 \pm 0.025 *
<i>n</i>	47	11	47	11
Exposure	365	95	365	95
Nestling Stage				
Year	Daily Survival Rate		Survival for Entire Period	
	Non-parasitized nests	Parasitized nests	Non-parasitized nests	Parasitized nests
2001	0.992 \pm 0.008	1.000 \pm 0.000	0.901 \pm 0.006 ***	1.00 \pm 0.00 ***
<i>n</i>	13	2	13	2
Exposure	158	23	158	23
2002	0.945 \pm 0.027	0.606 \pm 0.214	0.478 \pm 0.022 **	0.001 \pm 0.171 **
<i>n</i>	11	2	11	2
Exposure	87	7	87	7
Combined	0.975 \pm 0.011	0.924 \pm 0.051	0.717 \pm 0.009 ***	0.360 \pm 0.045 ***
<i>n</i>	24	4	11	2
Exposure	245	30	87	7
Overall Nesting History				
Year	Non parasitized nests		Parasitized nests	
	Year	Non parasitized nests	Parasitized nests	
2001	0.318 \pm 0.010 ***	1.000 \pm 0.000 ***		
<i>n</i>	30	2		
Exposure	402	49		
2002	0.233 \pm 0.015	0.001 \pm 0.350		
<i>n</i>	17	9		
Exposure	208	76		
Combined	0.286 \pm 0.008 ***	0.165 \pm 0.022 ***		
<i>n</i>	47	11		
Exposure	610	125		

Table 8. Daily and overall survival rates of Yellow Warbler and Shiny Cowbird eggs from parasitized and non-parasitized Yellow Warbler nests in Boquerón, Puerto Rico, 2001-2002. Survival is expressed in egg-days.

Year	Mean (\pm SE) egg survival rate					
	Daily Survival Rate			Survival for Entire Period		
	YWAR eggs Non-parasitized	YWAR eggs Parasitized	SHCO eggs	YWAR eggs Non-parasitized	YWAR eggs Parasitized	SHCO eggs
2001	0.894 \pm 0.015 ***	1.000 \pm 0.000 ***	1.000 \pm 0.000	0.261 \pm 0.018 ***	1.000 \pm 0.000 ***	1.000 \pm 0.000
<i>N</i>	78	6	3	78	6	3
Exposure	349	65	30	349	65	30
2002	0.920 \pm 0.017	0.882 \pm 0.269	0.884 \pm 0.036	0.368 \pm 0.033 ***	0.221 \pm 0.024 ***	0.226 \pm 0.032
<i>N</i>	25	22	13	25	22	13
Exposure	125	165	88	125	165	88
Combined	0.904 \pm 0.011	0.916 \pm 0.019	0.916 \pm 0.026	0.297 \pm 0.016 *	0.350 \pm 0.017 *	0.350 \pm 0.024
<i>N</i>	103	28	16	103	28	16
Exposure	474	230	118	474	230	118

Table 9. Daily and overall survival rates of Yellow Warbler and Shiny Cowbird chicks from parasitized and non-parasitized Yellow Warbler nests in Boquerón, Puerto Rico, 2001-2002. Survival is expressed in chick-days.

Year	Mean (\pm SE) chick survival rate					
	Daily Survival Rate			Survival for Entire Period		
	YWAR chicks Non-parasitized	YWAR chicks Parasitized	SHCO chicks	YWAR chicks Non-parasitized	YWAR chicks Parasitized	SHCO chicks
2001	0.989 \pm 0.006 **	0.455 \pm 0.195 **	1.000 \pm 0.000 **	0.867 \pm 0.005 ***	0.000 \pm 0.145 ***	1.000 \pm 0.000 ***
<i>n</i>	30	4	3	30	4	3
Exposure	343	11	41	343	11	41
2002	0.944 \pm 0.019 **	0.544 \pm 0.152 **	0.821 \pm 0.080	0.471 \pm 0.037 ***	0.000 \pm 0.116 ***	0.077 \pm 0.073
<i>n</i>	24	5	4	24	5	4
Exposure	71	16	25	71	16	25
Combined	0.974 \pm 0.008 ***	0.509 \pm 0.120 ***	0.929 \pm 0.034 ***	0.706 \pm 0.008 ***	0.000 \pm 0.091***	0.385 \pm 0.029 ***
<i>n</i>	54	9	7	54	9	7
Exposure	414	27	66	414	27	66

DISCUSSION

Breeding biology parameters obtained from this study, such as duration of breeding season, nest site selection habits, mean clutch size for non-parasitized nests, and dates of maximum hatching and fledging coincided with those found by Prather and Cruz (1995) for the Cuban YWAR (*D. p. gundlachi*) nesting in the Florida Keys. This was the only account found on the breeding biology of a Caribbean subrace, and this population was not being parasitized at the moment of the investigation.

The combined effects of high predation and parasitism rates imposed a considerable burden on the YWAR population at Boquerón. Predation accounted for the vast majority of nest losses during both years. Non-parasitized nests were predated mostly during the incubation stage, while most parasitized nests were predated during the nestling stage. Even though some nest losses were easily attributed to common nest predators, such as rats or monkeys, in other cases, nest destruction by cowbirds could not be ruled out. Brown-headed Cowbirds are known to destroy nests found late in the nesting cycle to force hosts to renest, thus generating new chances for parasitism (Arcese *et al.* 1996). Similarly, evidence suggests that cowbird presence in an area is associated to a reduction in egg survival and hatching success for non-parasitized nests when compared with nests from a cowbird free area. Massoni and Reboreda (2002) suggest that Shiny Cowbirds puncture host eggs while inspecting nests to determine embryo development and opportunities for successful parasitism.

The presence of parasite eggs or chicks has been repeatedly linked with higher predation rates at parasitized nests (Massoni and Reboreda 1998; McLaren and Sealy 2000). One possible explanation for this is nest vulnerability, namely, nests that are easily found by SHCO females could be readily found by a nest predator using similar cues during nest searching. However, this hypothesis predicts that parasitized nests are equally predated at all nesting stages. While this may be true, in the present study most parasitized nests were lost during the nestling stage. The higher predation of parasitized nests versus non-parasitized nests during the nestling stage could be explained by the SHCO chicks intense

begging and noisiness, which could draw attention of predators to the nest. In general, predation was very intense during 2002, and there is a possibility that more regular nest inspections by the researcher facilitated the finding of nests by predators during the second year. Nest predators in the area might include: Black rats (*Rattus rattus*), feral cats (*Felis catus*), Rhesus (*Macaca mulatta*) and Patas (*Erythrocebus patas*) monkeys, Smooth-billed Ani (*Crotophaga ani*) common anole (*Anolis cristatellus*), among others.

Less frequent nest inspections during 2001 may have underestimated parasitism, as nests that were deserted shortly after parasitism or in which cowbird eggs were buried between visits were most likely missed. Thus, I believe 2002 observations are more representative of the actual parasitism pressure in BCF. Compared to the 1977-1980 observations (Wiley 1985), when almost all nests were parasitized, parasitism frequency and pressure have decreased significantly. In addition, YWAR mean clutch size and YWAR fledged from successful nests has increased. However, parasitism is still high enough ($\geq 50\%$) to affect a considerable proportion of YWAR nests. These findings are consistent with a decline in parasite numbers around the BCF as a result of cowbird trapping around the managed area, and should not be confused with a reduction in individual parasite intensity on YWAR nests.

In fact, López-Ortiz *et al.* (2006) suggest a shift in SHCO host preference toward the YWAR in the managed area, explained by imprinting of individual cowbirds at the nest. Parasite removal from YSBL nests since 1991 might be the origin of this change. Since cowbird eggs and chicks have been removed exclusively from YSBL nests in BCF, cowbirds that fledge from other hosts, such as the YWAR, are more likely to parasitize these during adulthood. It follows that a higher proportion of cowbird eggs will end in YWAR nests than in YSBL nests.

Cowbirds parasitized susceptible nests at an estimated rate of 0.14 ± 0.06 cowbird eggs laid per day. Pease and Grzybowski (1995) expected the daily parasitism rate to be proportional to cowbird densities, with more nests being parasitized daily as cowbird numbers increased. Most parasitic events were observed when the proportion of susceptible nests was higher. Moreover, nest survival rates for

parasitized nests were much lower than for non-parasitized nests. YWAR egg survival for 2002 was much lower for parasitized nests. The opposite was observed in 2001, but this is probably due to small sample size (two parasitized nests that survived until fledging of SHCOs). About 50% of YWAR chicks were lost daily at parasitized nests; in other words, YWAR chicks in parasitized nests did not survive for more than two days. In addition, YWAR eggs from parasitized nests lasted as long as SHCO eggs in those same nests. This means that egg survival of YWAR and SHCO were only subject to predation and there was no difference in survival between them.

Although parasitism affects the YWAR at all stages, the more adverse effect of parasitism occurs during the nestling stage. SHCO chicks, hatching earlier and begging more strongly, easily outcompete their YWAR nestmates for adult attention. Apparently, adult feeding is biased toward the larger chick at the nest (Briskey and Sealy 1987), or to the chick that reaches higher and positions itself closer to the feeding parent (Lichtenstein and Sealy 1998). Whatever the explanation, the presence of a cowbird chick at the nest guaranteed the loss of the entire YWAR clutch, as no nest fledged cowbird and warbler chicks simultaneously.

In about three decades, since SHCO arrival to southwestern Puerto Rico, the YWAR has developed responses to counteract parasitism. Antiparasite defense mechanisms have been classified as those to prevent parasitism and those occurring after the nest has been parasitized (Rothstein 1975; Ortega and Cruz 1991). On several occasions I observed defensive behaviors around the nest that could be aimed at cowbirds to prevent parasitism. Examples are females sitting down in the nest with wings spread protecting the eggs and refusing to leave the nest when approached, or showing aggressiveness toward the investigator. However, these should be tested to differentiate antiparasite defenses from those against predation.

The YWAR presented a high degree of rejection toward parasitism (43-50% of parasitized nests). Only two nest desertions were observed in this study, and these occurred on nests which were previously parasitized and buried. Early nest desertions resulting from parasitism might have been missed, either

due to higher chances of predation of these nests or to adults using nest materials to renest elsewhere. In addition, the presence of female cowbirds before egg laying may cause the desertion of nests. Since these nests were not considered active, they were not included in the sample.

Wiley (1985) found YWAR nest desertion rates to be inversely related to number of host eggs at the moment of parasitism during 1975-1981. He also found nest desertion rates for parasitized YWAR nests at Boquerón to be significantly higher than for non-parasitized nests. In addition, Roosevelt Roads warblers did not lay eggs in nests where a SHCO had laid the first egg, with desertion of these accounting for 65% of nest failures. Wiley does not report egg burial at any of these nests.

To my knowledge, this is the first report of cowbird eggs burial by the YWARs in Puerto Rico and possibly the Caribbean. Data suggests that the response to parasite eggs in the nest is determined by YWAR investment at the moment of parasitism. In all nests parasitized before the window of susceptibility to parasitism (i.e., no warbler eggs), adults buried cowbird eggs under nest lining, while nests parasitized inside or after the window (i.e., 1-3 eggs) accepted parasitism. It follows that cowbirds have to parasitize nests in a period of 3 to 4 days to be successfully accepted.

Clearly, rejection mechanisms are a response to the high parasitism pressure suffered since 1970's. The immediate appearance of responses against parasitism in the YWAR relative to other species is explained by the species wide distribution in the New World. Although Caribbean races had not experienced brood parasitism before the arrival of the SHCO, it is likely that their ancestors from the continental Americas had. 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. Thus, when strong parasitism pressure was experienced by SHCO arrival, YWAR were able to respond more readily than other species. This study demonstrates that YWAR anti parasitic behavior in Puerto Rico might not be different from what is observed in regions where cowbirds and warblers have coexisted for a long time.

CONCLUSIONS

- About a third of YWAR nesting attempts at BSF were successful. Major causes of nest failure were predation and SHCO parasitism.
- The YWAR was a frequently parasitized species at Boquerón, with a parasitism pressure of at least 67%.
- The SHCO trapping program has partially benefited other species than the YSBL by decreasing parasite density, thus reducing parasitism frequency and number of SHCO eggs per parasitized nests.
- The high parasitism pressure experienced by the YWAR represented a strong stimulus that may have evoked the expression of pre existing anti parasite mechanisms in this species. Apparently, YWAR rejection of parasite eggs resulted in a reduced success of SHCOs at parasitized nests.

RECOMMENDATIONS

Based on the results of this study the perpetuation of the SHCO control program in BCF is recommended. The YWAR and probably other species have partially benefited from the trapping of SHCO in terms of a reduction in cowbird numbers around the BCF. It would also be advisable to include the YWAR and other native species that suffer a higher parasitism pressure than the YSBL itself as focal species to the management program (i.e. removal of cowbird eggs and chicks from nests).

No YWARs outside the managed area were observed, but one could expect that populations not subject to a cowbird control program face higher parasitism rates than those in BCF. Higher parasitism rates in these areas might result in the disappearance of the YWARs before any rejection behavior could be established in the population. Thus, it is imperative to extend the SHCO control and capture program outside the managed area.

It should be pointed out that these are just temporary measures to maintain YWAR numbers until more permanent, long-term fixes are implemented. Since forest degradation and fragmentation are at the base of the expansion and establishment of the SHCO on new areas, these issues should be addressed immediately by the wildlife authorities. Although parasitism affects YWAR breeding success considerably, this species has responded with defenses to cope with this threat. However, the YWAR is unable to respond to mangrove and coastal habitat loss and degradation throughout the island. Therefore habitat protection, restoration and enhancement are advised for the conservation of this species.

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