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REDUCTION IN HOST USE SUGGESTS HOST SPECIFICITY IN INDIVIDUAL SHINY COWBIRDS (*MOLOTHRUS BONARIENSIS*)

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Resumen. – Reducción en el uso de hospedero sugiere especificidad de hospedero en individuos de Tordos Lustrosos (*Molothrus bonariensis*). – La Mariquita de Puerto Rico (*Agelaius xanthomus*) está en peligro de extinción, principalmente como resultado del parasitismo de camada por el Tordo Lustroso (*Molothrus bonariensis*). Para mitigar los efectos del parasitismo, se implementó a largo plazo un programa de control de tordos, dirigido a atrapar tordos (tratamiento 1) y remover sus huevos y pichones de los nidos de mariquitas (tratamiento 2). El programa está concentrado en el suroeste de Puerto Rico donde la Mariquita de Puerto Rico y el Canario de Mangle (*Dendroica petechia*) son los hospederos más importantes. En el área manejada, el porcentaje promedio de parasitismo de camada en nidos de la Mariquita de Puerto Rico y del Canario de Mangle fue de 3 y 42%, respectivamente. En un área de referencia (sin programa), el porcentaje en la mariquita promedió 54% mientras que observamos 85% de los nidos del canario parasitados. El contraste en los porcentajes de parasitismo es sorprendente porque la mariquita fue previamente reconocida como el principal hospedero, y porque los tordos son comunes en el área estudiada. La diferencia en porcientos de parasitismo entre áreas fue atribuida al entrampamiento. Investigamos si el tratamiento 2 pudiera resultar en una reducción del uso del hospedero, aun en abundancia de tordos y nidos del hospedero. Para esto, predijimos que una tasa alta de parasitismo en los nidos de canario, pero baja en los nidos de mariquita, podría sugerir que los resultados no fueron causados exclusivamente por el tratamiento 1; si no, esperaríamos que el entrampamiento tuviera efectos similares en ambos hospederos. Esto deja el tratamiento 2 como el factor ejerciendo influencia en la selección del hospedero, por ende, una prueba apropiada para posible especificidad de hospedero. Nuestros resultados sugieren que el tratamiento 2 redujo significativamente el uso de un hospedero, quizás por no permitir la improntación de la Mariquita de Puerto Rico como hospedero.

Abstract. – The Yellow-shouldered Blackbird (*Agelaius xanthomus*) is endangered, mainly as a result of brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*). To reduce the effects of parasitism, a long-term cowbird control program was implemented, aimed at trapping cowbirds (treatment 1) and removing their eggs and chicks from blackbird nests (treatment 2). The program is concentrated in southwestern Puerto Rico, where Yellow-shouldered Blackbirds and Yellow Warblers (*Dendroica petechia*) are the most important cowbird hosts. In the managed area, the average percentage of broods parasitized in nests of Yellow-shouldered Blackbirds and Yellow Warblers was 3 and 42%, respectively. In a reference area (no program), the percentage of parasitized blackbird nest averaged 54% whereas we observed 85% of warbler nests parasitized. The contrast in parasitism percentages is noteworthy because the blackbird was previously recognized as the main host, and because cowbirds are common in the studied area. The difference

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in parasitism percentages between areas was attributed to the trapping. We investigate if treatment 2 would result in a reduction of host use, even in abundance of cowbirds and host nests. For this, we predicted that a high parasitism rate of warbler nests, but low for blackbird nests, would suggest that results were not caused exclusively by treatment 1; otherwise, we would expect trapping to have similar effects on both hosts. This leaves treatment 2 as the factor exerting influence on host selection, hence, an appropriate test of possible host specificity. Our results suggest that treatment 2 decreased significantly a host use, perhaps by not allowing the imprinting of a Yellow-shouldered Blackbird as a host. *Accepted 12 January 2006.*

Key words: *Agelaius xanthomus, Dendroica petechia,* host selection, *Molothrus bonariensis.*

INTRODUCTION

The Shiny Cowbird (*Molothrus bonariensis*) is an obligate brood parasite, native to South America, Trinidad and Tobago, that has expanded its range into the West Indian region (Post & Wiley 1977, Cruz *et al.* 1985, 1989; Lowther & Post 1999). This bird probably reached Puerto Rico by "island hopping" through the Lesser Antilles during the 1940s, parasitizing populations of Yellow Warblers (*Dendroica petechia*) (Friedmann *et al.* 1977, Post & Wiley 1977), although it was first reported in Puerto Rico in 1955 (Grayce 1957). Similar to the well-studied Brown-headed Cowbird (*M. ater*), the Shiny Cowbird (henceforth SHCO) has been reported to use over 200 host species (Friedmann & Kiff 1985, Ortega 1998).

In Puerto Rico, Yellow-shouldered Blackbirds (*Agelaius xanthomus*) and Yellow Warblers are considered high-quality host species (Wiley 1988). From 1975 to 1983, 91% of Yellow-shouldered Blackbirds and 63% of Yellow Warblers nests studied were parasitized (Cruz *et al.* 1989). The high incidence of parasitism found in blackbird nests of lowland Puerto Rico ranked it as the primary host (Post & Wiley 1977, Cruz *et al.* 2005).

The Puerto Rico Department of Natural and Environmental Resources (PRDNER 2004), the United States Fish and Wildlife Service (USFWS 1996), and the International Union for Conservation of Nature (IUCN 2001) considered the Yellow-shouldered Blackbird (henceforth YSBL) as an endangered species. Brood parasitism was identified as the primary factor contributing to the decline of YSBL in the second half of the 20^{th} century (Post & Wiley 1976, 1977; Cruz *et al.* 1985, Wiley 1985, Cruz *et al.* 2005). The largest population in Puerto Rico occupies the mangrove swamps of southwestern Puerto Rico (Fig. 1), primarily the Boquerón State Forest (henceforth BSF). In 1982, the PRDNER, through a cooperative agreement with the USFWS, initiated a control program aimed at trapping SHCO and monitoring YSBL reproduction in southwestern Puerto Rico (Wiley *et al.* 1991, USFWS 1996, Cruz *et al.* 2005). From 1993 until present, the program mainly used repeat-capture traps strategically distributed at Pitahaya (a sector within the BSF - the main YSBL breeding ground) and in the main feeding grounds of SHCO around the BSF (Fig. 1). Starting in 1991, SHCO eggs and chicks were removed from YSBL artificial nest structures to enhance the host's reproductive success, and this strategy is still in practice. From 1996 to 1999, only 2.7% of 858 YSBL nests were parasitized within the BSF, and no significant difference in parasitism rates were detected between artificial nest structures and nests in natural substrates. Almost every YSBL nest was purged of SHCO eggs or chicks during that period (López-Ortiz *et al.* 2002).

The success of the control program and its long duration (Cruz *et al.* 2005) presented an opportunity to test hypotheses about host

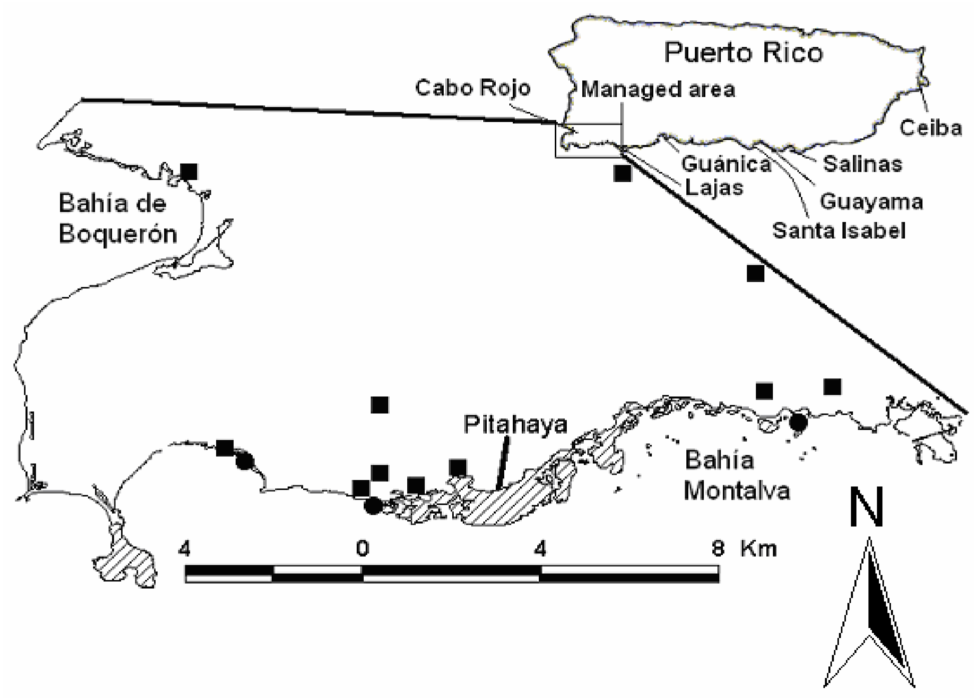

FIG. 1. Puerto Rico showing the study area, including managed area (BSF; striped zones), reference area (Ceiba, Guánica, Guayama, Salinas and Santa Isabel), area of Shiny Cowbird eggs and chicks removal (Pitahaya), Shiny Cowbird traps (black squares) and blackbirds' roosts within the BSF (black dots).

selection by SHCO. Specifically, we were interested in determining if treatment 2 (cowbird egg and nestling removal) would result in a reduction in host use even with abundance of cowbirds and host nests. This may clarify if individual SHCO are being specific toward a host species. Additionally, although behavioral imprinting in avian brood parasites has only been reported in captive *Vidua* finches (Nicolai 1964, 1974; Payne *et al.* 1998, 2000; Sorenson *et al.* 2003), we were also interested in evaluating if a reduction in host use by SHCO could be a result of imprinting. In this model, an adult SHCO will preferentially parasite hosts of the same species as its foster parents. It follows that host selection is intimately related to host nest success in producing SHCO fledglings.

To test these hypotheses (reduction in host use and imprinting), we first tested the null hypothesis of no difference in the percentages of YSBL or Yellow Warbler (henceforth YWAR) nests parasitized between a managed area with SHCO control program and a reference area with no control program. The YWAR was the other high-quality host species, relatively abundant and nesting near YSBL, mainly within black mangrove (*Avicennia germinans*) patches. The paired approach permitted a SHCO to make a choice between both high-quality host species and ensured that habitat characteristics were similar, thus, not a confounding factor (see Post & Wiley 1977, Gates & Gysel 1978, Chace *et al.* 2002). We predicted that a higher frequency of parasitism in the reference area would suggest that the control program contributed to reduce parasitism rates.

We also tested the null hypothesis of no difference in parasitism within the managed area between the two host species. We predicted that a high parasitism percentage of YWAR nests but low for YSBL nests (as found from 1996 to 1999; Lopez-Ortiz *et al.* 2002) would suggest that results were not exclusively caused by treatment 1 (trapping cowbirds); otherwise, we would expect trapping to have similar effects on both hosts. This leaves treatment 2 as the factor exerting influence on host selection and host specificity, hence, an appropriate test of possible imprinting. We assumed that imprinting functions as recently described by Hoffman (1996). In other words, imprinting is neither rapid nor irreversible, and for this kind of social bonding to occur, the imprinted subject provided stimulation that was pleasurable and comforting enough to innately stimulate the production of endorphins, just as in parental care by foster parents.

STUDY AREA

We conducted this study mainly along the coast of southern Puerto Rico, between the municipalities of Cabo Rojo and Salinas and the municipality of Ceiba (Fig. 1). The managed or treatment area was defined as the coastal fringe from Bahía de Boquerón at Cabo Rojo to Bahía Montalva in the municipality of Lajas at the eastern end, primarily within the BSF. The habitat within the BSF is preserved; therefore, for a detailed description, see Wiley (1985). The reference area was defined as the coastal fringe from the municipality of Guánica in the west to the southeastern municipality of Salinas and mangroves within the Roosevelt Road Naval Station at the municipality of Ceiba, eastern Puerto Rico (Fig. 1). The reference area contained (Fig 1; Ceiba, Guánica, Guayama, Salinas and Santa Isabel) four pre-surveyed small populations of YSBL (USFWS1996), probably the only population remnants beside Mona and Monito Islands (islets between Puerto Rico mainland and Hispaniola) and southwestern Puerto Rico.

METHODS

We meticulously searched for YSBL and YWAR active nests (nest containing host or SHCO eggs or nestlings), in the reference and managed areas, from May to August of 2000, 2001, and 2003. We monitored every YSBL (in artificial nest structures and natural substrates) and YWAR nest weekly to determine the presence of SHCO eggs or chicks. Whereas blackbirds and other species congregate in large groups within their roosting sites, we counted the SHCO as they entered or left the roosts within the BSF to estimate their abundance (Post & Wiley 1976, Post 1982, Post & Post 1987). Counts were conducted during two mornings (06:00-08:00) and two afternoons (16:00–19:00) during three consecutive days, before (March) and after (August) the YSBL reproductive seasons of 2000, 2001, and 2003.

The parasitism proportions were transformed with ARCSINE, a recommended transformation for percentages and proportions (Sokal & Rohlf 1995) to analyze differences in a two-way ANOVA with the computer program SPSS (1999) for MS Windows. With the same computer program, chi-square tests were used to compare the incidence of parasitism before and after the cowbird control program was implemented, between the managed and the reference area, and between hosts. For further comparisons the raw data are presented. Descriptive statistics are given as mean and standard deviation (SD) and significance was set at 0.05.

TABLE 1. Number of active and parasitized nests of Yellow-shouldered Blackbirds (YSBL) and Yellow Warblers (YWAR) in reference (municipalities of Cabo Rojo and Lajas) and managed (municipalities of Ceiba, Guánica, Guayama, Salinas, and Santa Isabel) areas during the summer of 2000, 2001, and 2003.

Species	Year	Active[1]	Reference parasitized	%	Active	Manages parasitized	%
YSBL	2000	18	8	44	296	0	0
YSBL	2001	2	1	50	325	12	4
YSBL	2003	12	5	42	306	17	6
Annual Mean	2001-03	11	5	45	108	10	3
YWAR	2000				14	7	50
YWAR	2001				82	15	18
YWAR	2003	13	11	85	69	39	57
Annual Mean	2001-03	13	11	85	55	20	42

[1]Nests with eggs and/or chicks.

RESULTS

The area intensively surveyed within black mangrove forests followed a zigzagged pattern of 2.5 and 2.4 km^2 in the reference and managed area, respectively. Within the managed area, the YSBL and YWAR nests were within 400 m from each other. In contrast, no YSBL nest was found within the black mangrove forests at the reference area. Within the reference area, YSBL nests were found only in suburban and industrial environments at Ceiba, Guánica, Guayama, and Salinas with reproductive data available only from nests at Ceiba (at approximately 56 km from Guayama), Guánica (at approximately 80 km from Guayama), and Guayama (Fig. 1). The average annual parasitism in YSBL nests within the managed and reference area was 3.3% (SD = 3.1) and 45.3% (SD = 4.2), respectively (Table 1). The average annual parasitism in YWAR nests within the managed area was 41.7% (SD = 20.8), whereas 85.0% was found in the reference area (Table 1; 2003). These percentages differed significantly between area and between host species (Two-way ANOVA; Table 2). The percentages were higher at the reference area in both species (Tables 1 and 2). When the species were tested individually between areas, the percentages in YSBL nests differed significantly (χ^2 = 174.241, df = 1, $P < 0.001$), as did YWAR (χ^2 = 287.737, df = 1, $P < 0.001$).

The difference between species in the percentages of parasitized nests was significant within the managed area (χ^2 = 623.539, df = 1, $P < 0.001$) and within the reference area (χ^2 = 41.051, df = 1, $P < 0.001$), and the YWAR nests had a higher incidence of parasitism in both areas (Table 1).

We compared the overall parasitism found within the managed areas with the parasitism reported in YSBL and YWAR nests before cowbird control was implemented (Cruz *et al.* 1989). The following parasitism percentages are given for Ceiba, and BSF, respectively. From 1975–76, brood parasitism was found in every YSBL nest (n = 18 and 35). Similarly, from 1980–83, brood parasitism was found in all (n = 14) and 97% (n = 93) of the YSBL nests. In YSBL nests within the managed areas, the overall percentages were higher before the control program was implemented (χ^2 = 25.176, df = 1, $P < 0.001$).

In YWAR nests, the overall parasitism percentages found were 11% (n = 19) and zero (n = 3), from 1975–76. From 1980–83, brood parasitism was found in 91% (n = 34)

TABLE 2. Two-way ANOVA comparing parasitism between species (Yellow-shouldered Black Bird and Yellow Warbler) and areas during the summer of 2000, 2001, and 2003. Managed areas are within the municipalities of Cabo Rojo and Lajas and reference areas within the municipalities of Ceiba, Guánica, Guayama, Salinas, and Santa Isabel.

Source	Sum of squares	df	Mean square	*F*	Sig.
Corrected model	0.799	3	0.266	14.795	0.004
Intercept	1.915	1	1.915	106.355	0.000
Species	0.450	1	0.450	24.992	0.002
Areas	0.517	1	0.517	28.686	0.002
Species*areas	1.000E-02	1	1.000E-02	0.555	0.484
Error	0.108	6	1.801E-02		
Corrected total	0.907	9			

and 23% (n = 48) of the YWAR nests. These percentages were similar to the ones found within the managed areas (χ^2 = 1.926, df = 1, P = 0.165).

We also compared the overall percentages of parasitism in the reference area to the parasitism reported before management, from 1975 to 1983 (Cruz *et al.* 1989). The YSBL reference parasitism was significantly lower than the percentages before management (χ^2 = 198.597, df = 1, P < 0.001). The YWAR reference percentage was higher to the percentage before management (χ^2 = 57.909, df = 1, P < 0.001).

In 1998, 22 SHCO eggs were removed from YSBL artificial nest structures. This is particularly interesting because every egg was characterized by having a light blue background color instead of bone white as usual.

At roost sites, during March 2000, 2001, and 2003, 148, 91, and 148 SHCO were counted, respectively. During August 2000, 2001, and 2003, 1042, 538, and 1097 SHCO were counted, respectively. Therefore, on average the population of SHCO using the roost sites increased 6.79 (SD = 0.78, n = 3) times in each reproductive season.

DISCUSSION

***Managed vs reference areas*.** We believe that almost all active YSBL nests were monitored. As the managed and reference areas surveyed are probably the only population remnants within the Island, we conclude that the sample size was close to the total population of YSBL nests in Puerto Rico. Although the YSBL nests sample size was smaller in the reference area, the small population size surveyed at roosting sites assure that it was indeed representative. Even though nests of YWAR were more inconspicuous and less aggregated than blackbird nests (Cruz *et al.* 1985, 1989), the search effort was thorough enough to ensure that the sample size was also representative of the studied areas.

The relatively high percentage of parasitized YSBL nests (52%) in the reference area compared to the managed area (3%) did not occur by chance alone (i.e., significant two-way ANOVA). The long-term effect of removing cowbirds and their offspring within the managed area most likely caused the difference in parasitism between areas. Before management (1973–1982), the parasitism percentage reported for YSBL in the BSF was 95% (191/202) (Wiley *et al.* 1991, Cruz *et al.* 2005). We believe that although the parasitism pressure was lower in the reference area, it has not changed considerably from pre-management figures in BSF. Perhaps the statistical difference may be attributed to differences in habitat. Although we try a paired approach to ensure that habitat characteristics were similar, YSBL nests found within the reference areas were in upland and not in mangrove habitat, a factor that may influence the availability of YSBL nests to SHCO (Post & Wiley 1977, Gates & Gysel 1978, Chace *et al.* 2002). On the other hand the reduced size and the spaced distribution of the population remnants could affect the availability of these nests to the SHCO population (see Wiley 1985).

The parasitism percentage recorded in two high-quality host species within the managed area is mainly the result of the SHCO control program. In 7 years (including from 1996 to 1999; López-Ortiz *et al.* 2002), we recorded low parasitism percentages in YSBL nests within the managed area. Furthermore, the average parasitism recorded in YWAR nests within the managed area in 2000, 2001, and 2003 was half (0.42) the percentage found in 2003 (0.85) in similar areas with no SHCO control. An earlier study (Cruz *et al.* 1985) suggests that the parasitism rate found in YWAR was higher before management. From 1975 to 1982, 64% of the YWAR nests were parasitized in the BSF (Cruz *et al.* 1985).

Within the managed area, YWAR nests were more heavily parasitized than the YSBL nests. The difference in parasitism percentage between host nests was unexpected if we assumed that treatment 1 alone was responsible for reducing parasitism percentages. This contrasts to earlier parasitism percentages which were higher in YSBL than in YWAR nests in areas where they were found together (Cruz *et al.* 1989). From 1975 to 1976, all (n = 53) YSBL nests and 9% of the YWAR nests (n = 22) were parasitized at Roosevelt Road Naval Station and BSF. Similarly, from 1980 to 1983, parasitism percentages of 97% and 29% were found in nests of YSBL (n = 107) and YWAR (n = 82), respectively.

*Reduction in host use***.** Our study suggests that removal of cowbird offspring from blackbird nests has resulted in a reduced use of the main host of the SHCO. From 1991 to 2003, every SHCO egg or chick has been removed from the YSBL artificial nest structures, causing a drop to near zero parasitism in YSBL nests within the managed area (Cruz *et al.* 2005, López-Ortiz *et al.* 2002). Thus, hosts other than the YSBL reared SHCO chicks within the managed area.

In an earlier study, Wiley (1985) suggested that host shifting in the Shiny Cowbird might be caused by the scarcity of the primary host, the YSBL. This appears to be the case in the reference areas of mangrove habitat, where no YSBL nests were found and YWAR has become the principal SHCO host. On the contrary, this is unlikely in the managed area, as the YSBL population in BSF has increased from an estimated population of 300 individuals in 1981–1982 (Wiley *et al.* 1991) to a population close to 800 individuals (Cruz *et al.* 2005). The high number of YSBL nests encountered, the proximity between YWAR and YSBL nests (within 400 m in the managed area), and the proximity of nests of both species to SHCO roost sites, imply that nests of both species were effectively available to the SHCO. The reduction in the use of YSBL as a host should not be related to SHCO surveillance during the act of offspring removal by researchers and subsequent host avoidance. Because, in contrast to old world cuckoos (Zahavi 1979), SHCO lays and abandons the eggs (but see Sealy 1992, Lorenzana & Sealy 1998). Our findings also suggest that this reduction in host use should be the result of individual host specificity and probably host imprinting. Thus, a SHCO raised by YWAR would, as an adult, prefer to parasitize a YWAR nest.

*Host specificity***.** Brood parasitism is generally analyzed at the population level often neglecting the differences among the parasitism habits of individual parasites. However, research at the individual level can display important information on host composition and parasitism strategy. As confirmed by several works based in niche theory and the generalist-specialist dichotomy, a population with a narrow niche width must necessarily be composed of individuals with either narrow or wide niches, or a combination of both (i.e., Putman & Wratten 1984, Pianka 1988, Amundsen *et al.* 1996). Therefore, a broad niche width may be the result from either a true generalist behavior of each individual of a population on different hosts (high within individual variation) or a specialization of the individuals of the population on different hosts (high between individual variation).

Studies in the related Brown-headed Cowbird suggest that some individual females may be host specialists (Walkinshaw 1949, McGeen & McGeen 1968, Alderson *et al.* 1999). In the Brown-headed Cowbird, each female's eggs are more similar to one another than to cowbird eggs in the local population in size, color and pattern of spots (Dufty 1983, Payne 1998). Some researchers reviewed by Gibbs *et al.* (1997) suggested that Brown-headed Cowbirds may act as host specialist based on the observation of cowbird and hosts eggs morphology. Typically, SHCO eggs are easily differentiated from the YSBL eggs because the formers possess a white background color and a smaller size (Post & Wiley 1977). But, as observed by Post & Wiley (1977), we have found a few SHCO eggs with a light-blue background color, which make them quite similar to the YSBL eggs. The 22 bluish SHCO eggs found only in YSBL artificial nest structures during 1998 also suggest individual host specialization, because it is probable that those eggs came from the same flock or the same female.

Imprinting hypothesis. Mayfield (1960) suggested that cases of parasitic specialization of individual birds in generalist species (e.g., cowbirds) might be related to imprinting or learning of the host during parental care (see Friedmann & Kiff 1985). Recently, Gibbs *et al.* (1997) did not detect different races among young Brown-headed Cowbirds that were reared in nests of different hosts. Later Alderson *et al.* (1999) found that half of the female Brown-headed Cowbirds laid their eggs in the nests of the Red-winged Blackbird (*A. phoeniceus*). These two results, obtained in the Delta Marsh of Manitoba, are indeed expected within the imprinting hypothesis. Genetic difference is not likely at the race level because imprinting may change from one generation to another (Payne 1977). In addition, it is expected a higher use of imprinted hosts. The use of the imprinted host will also depend on its availability to cowbirds (e.g., a small remnant population of a couple of YSBL may not be available to the few cowbirds raised, and therefore imprinted, by the same couple during the previous breeding season). The imprinting hypothesis can be proved genetically if the proportion of host species used by sibling cowbirds, within the same generation period, is compared against the proportion of the same host species used at random. For such study the host species availability should be considered. The host species availability may depend on its intrinsic characteristics (e.g., nest type, nutritional needs, and aggressiveness toward cowbirds) and abundance, as well as habitat characteristics and cowbird abundance. No difference among the proportion of different hosts species used by sibling cowbirds at the same generation period might be expected in nesting habitats with high cowbird density (no control program) or few host nests available. Under such circumstances, a gravid female will be obligated to use any available nest, even a nest already used by another cowbird. This might be a difficulty to overcome in testing the proportion of hosts used by sibling cowbirds at Manitoba, where "the density of cowbirds was much higher than in other study populations" (Alderson *et al.* unpubl. *in* Gibbs *et al.* 1997).

Although SHCO have been characterized as host generalist (Ortega 1998), our results (obtained from host nests within the same habitat, with a SHCO control program and plenty of high-quality host nests), strongly imply that host specificity is occurring in this species at the individual level. This generalist species (at a population level) should consist of specialist individuals or a combination of specialist and generalist individuals. However, even the specialist individuals may change their strategy under extreme conditions where host specificity is impaired by the lack of the imprinted host. We searched fruitlessly in the published literature for comparative studies related to cowbird parasitism in study sites with a cowbird control program and plenty of high-quality host nests. The best comparable work was an unpublished study generously shared with us by J. W. Wiley (pers. com. with A. Cruz). In the next paragraph, we give a brief description of his work to further support our findings.

The J. W. Wiley study also provided strong support of host specificity and behavior development in SHCO when young are reared by different host species in Puerto Rico. At Roosevelt Roads Naval Station, Wiley did several cross-fostering manipulations among host species, involving Black-whiskered Vireos (*Vireo altiloquus*), Stripe-headed Tanagers (*Spindalis portoricensis*), YSBL, and YWAR in mangrove habitats. Approximately 60 cowbird nestlings were banded with unique combination of color leg bands at the nests of the above hosts, with the majority of nestlings banded at YWAR nests. During 18 months, the openness of the mangrove habitat allowed ease of observations of the banded birds and host nests. The extensive observations of host nests subsequently confirmed a host-specific individual strategy of these banded birds. Thus, SHCO which were raised by YWAR returned as adults to parasitize YWAR.

Our study, and the observation provided by Wiley, indicated that host specialization is occurring at the individual level. As we could not discard the imprinting hypothesis, our study suggests that imprinting, as the most parsimonious explanation, might play a role in host species selection in the SHCO. Interestingly, Friedmann & Kiff (1985) suggested that host imprinting might occur in SHCO in Puerto Rico on the basis of their high use of YSBL. As noted by Alderson *et al.* (1999) for Brown-headed Cowbirds, we suspect that, unlike old world cuckoos [e.g., Common Cuckoo (*Cuculus canorus*)] (Gibbs *et al.* 1996), patterns of host use by SHCO are plastic and subject to strong environmental influence. As suggested by recent advances in the study of imprinting, behavioral imprinting is not necessarily rapid or irreversible (Hoffman 1996). A comparison of the proportion of host species used by sibling cowbirds (of both genders) at the same generation periods, against a random use of host species considering their availability, will be useful to decipher if individual specificity through imprinting is a plastic strategy available to cowbirds.

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