ORNITOLOGIA NEOTROPICAL 15: 331–347, 2004

ACCEPTERS AND REJECTERS OF COWBIRD PARASITISM IN THE NEW WORLD ORIOLES (*ICTERUS* SPP.)

Spencer G. Sealy, & Todd J. Underwood

Department of Zoology, University of Manitoba, Winnipeg, Manitoba R3T 2N2 Canada.
E-mail: sgsealy@cc.umanitoba.ca

Resumen. – Aceptación y rechazo del parasitismo por tordos en los orioles del Nuevo Mundo (*Icterus* spp.). – Usando los orioles del Nuevo Mundo (*Icterus* spp.), probamos la hipótesis de Rothstein (1975), la cual sugiere que, en los tordos parasíticos, la aceptación o rechazo del parasitismo debería caracterizar a todos o a la mayoría de los miembros del taxón. Para ello, resumimos los resultados de otros estudios sobre parasitismo en orioles y revisamos la información disponible en parasitismo natural de tordos en otras especies, la cual clasifica las especies de orioles de acuerdo a su aceptación o rechazo al parasitismo por tordos, i.e., frecuencia del parasitismo, presencia de huevos de tordos al lado de los nidos y observaciones de orioles alimentando pichones y volantones de tordos. Adicionalmente, parasitamos experimentalmente otra especie de oriol, el Bolsero castaño (*I. spurius*), para determinar si esta acepta o rechaza el parasitismo por tordos. Los resultados de los experimentos conducidos por varios investigadores, los cuales simularon el parasitismo por tordos en los nidos de cinco de las 29 especies de orioles, revelaron que tres, o posiblemente cuatro, especies expulsan los huevos ajenos de sus nidos, mientras que una especie los acepta. En nuestros experimentos con los Bolseros castaños, estos aceptaron los huevos reales y artificiales de tordo en todos los nidos (n = 29). En conjunto con los resultados de otros estudios que han registrado altas frecuencias de parasitismo en muchas otras poblaciones del Bolsero castaño, nuestros resultados confirman que esta especie acepta el parasitismo por tordos. La biología reproductiva de siete especies de orioles es poco conocida, sin embargo, la información disponible en el parasitismo por tordos en otras 16 especies sugiere que la aceptación es posible o probable en 15 y la expulsión es posible en al menos una especie. Aunque especies diferentes de orioles aceptaron o rechazaron el parasitismo, la evidencia sugiere que la mayoría de las especies aceptan los huevos de tordo. Es necesario realizar más experimentos para confirmar estas afirmaciones; dichos resultados podrán ser usados en esfuerzos de conservación de aquellas especies que aceptan el parasitismo por parte de los tordos y por tanto son más vulnerables a los costos del parasitismo. De especial interés es el trabajo en aquellas especies que actualmente están experimentando nuevas amenazas de parasitismo, ya que los tordos expanden su rango y encuentran nuevas especies hospedadoras.

Abstract. – Using the New World orioles (*Icterus* spp.), we tested Rothstein's (1975) hypothesis that among hosts of parasitic cowbirds, rejection or acceptance of parasitism should characterize all or most members of a taxon. We accomplished this by summarizing the results of experimental cowbird parasitism on orioles, published chiefly by others, and reviewing available information on natural cowbird parasitism on other species of orioles that suggest their status as accepters or rejecters, i.e., the frequency of parasitism, presence of cowbird eggs beneath nests, and observations of orioles feeding nestling and fledgling cowbirds. We also experimentally parasitized another oriole species, the Orchard Oriole (*I. spurius*), to determine whether it accepts or rejects cowbird parasitism. Results of experiments that simulated cowbird (*Molothrus* spp.) parasitism on nests of five of the 29 species of orioles, conducted by various researchers, revealed that three or possibly four species eject the foreign eggs from their nests, whereas one species accepts them. Our experiments on the Orchard Oriole resulted in acceptance of real or model cowbird

eggs at all nests (n = 29). Coupled with high frequencies of parasitism recorded for many other populations of Orchard Orioles, these results confirm the Orchard Oriole as an accepter. The breeding biology of seven species of orioles is little known, but the information available on cowbird parasitism for 16 other species suggests acceptance is possible or probable for 15 and ejection is possible for at least one additional species. Both accepters and rejecters occurred among the orioles, but the evidence suggests most species accept cowbird eggs. Experiments are needed to confirm this and the results will assist conservation efforts on those species that accept cowbird parasitism and, hence, are most vulnerable to the costs of cowbird parasitism. Work is especially desirable on species that currently are experiencing new threats of parasitism, as cowbirds expand their range and encounter new host species. *Accepted 25 January 2004*.

Key words: Brood parasitism, cowbirds, *Molothrus* spp., Orchard Oriole, *Icterus spurius*, orioles *Icterus* spp., accepters, rejecters.

INTRODUCTION

Whether potential host species accept or reject cowbird (*Molothrus* spp.) eggs, or exhibit a mixture of these responses, is determined without bias by adding a real or model cowbird egg to their clutches and recording the fate of the foreign egg (Rothstein 1971, 1975). Routine inspections of unmanipulated nests may result in cowbird parasitism being underrecorded or not recorded, if cowbird eggs are ejected before or between nest inspections (Rothstein 1974, Scott 1977, Sealy & Bazin 1995). Cowbird eggs found during nest inspections that remain in active nests may lead to the conclusion that the species is an accepter, but nests at which no parasitism was recorded may have been parasitized and the eggs were ejected. Experiments on nests of these species will confirm that all individuals are accepters or that some are ejecters.

Rothstein (1975: 265) hypothesized that accepters and rejecters "should sort out along taxonomic lines, either rejection or acceptance being characteristic of all or most of the members of a taxon." When Rothstein conducted this work, clear patterns had not emerged among genera and families of birds because too few individuals and species had been tested. Results of recent experiments conducted on flycatchers (Tyrannidae) and thrashers (Mimidae) have provided mixed support for this hypothesis. The seven species of *Tyrannus* tested have been classified as ejecters (Peer & Sealy 2000), whereas five other flycatcher species among other genera accept cowbird eggs (Rothstein 1986, Briskie & Sealy 1987, Curson *et al.*1998, Underwood *et al.* in press, Sealy unpubl.). Of 11 species of mimids tested, two are accepters, seven are ejecters and two species exhibit an intermediate response to parasitism (Rothstein 1975, Finch 1982, Fraga 1985, Friedmann & Kiff 1985, Rich & Rothstein 1985, Carter 1986, Cruz *et al.* 1989, Haas & Haas 1998, Peer *et al.* 2002).

The 29 currently recognized species of *Icterus* (Sibley & Monroe 1990, AOU 1998, Baker *et al.* 2003) afford an excellent opportunity to test Rothstein's hypothesis. These species inhabit most of the New World from southern Canada to northern Argentina, with the greatest diversity occurring in Mexico where 14 species breed (Howell & Webb 1995). Collectively, the ranges of *Icterus* species overlap those of three species of brood-parasitic cowbirds – Brown-headed (*Molothrus ater*), Bronzed (*M. aeneus*) and Shiny (*M. bonariensis*) cowbirds (Friedmann *et al.* 1977) – and many authors have noted that orioles are important hosts of these parasites (e.g., Bendire 1895; Friedmann 1929, 1963; Thurber & Villeda 1980, Pleasants 1981, Skutch 1996; but see Sealy *et al.* 1998). Brown-headed Cow-

bird eggs added experimentally to clutches of Baltimore Orioles (*I. galbula*) and Bullock's Orioles (*I. bullockii*) were ejected from all or most nests by both species (Rothstein 1975, 1977, 1978; Rohwer *et al.* 1989, Røskaft *et al.* 1993, Sealy & Neudorf 1995). All Brown-headed Cowbird eggs added to nests of Hooded Orioles (*I. cucullatus*), on the other hand, were accepted (Friedmann *et al.* 1977). These results are consistent with Rothstein's (1975, 1976, 1977, 1982) experiments on about 50 species of potential hosts of the Brown-headed Cowbird in which most species either accepted or rejected the foreign eggs, with few species exhibiting intermediate levels of acceptance and rejection. This trend has been confirmed in many recent studies on species in several genera (e.g., Finch 1982, Rich & Rothstein 1985, Sealy & Bazin 1995, Peer & Sealy 2000). Most species of orioles remain to be tested before trends in responses to cowbird parasitism in this genus can be elucidated fully, but in lieu of these data, we summarized the available literature and conducted a field test to reveal responses to cowbird parasitism.

Our objectives were two-fold. First, we tested Rothstein's hypothesis that acceptance or rejection characterizes all or nearly all species of a taxonomic group, using the New World orioles (*Icterus*). To accomplish this, we summarized the results of experimental cowbird parasitism on orioles in the genus *Icterus*, published chiefly by others, and reviewed available information on natural cowbird parasitism on other species that suggested their status as accepters or rejecters. Our second objective was to test another oriole species, the Orchard Oriole (*I. spurius*), to determine whether it accepts or rejects cowbird parasitism.

We summarized the records of parasitism on other *Icterus* species by Bronzed Cowbirds and Shiny Cowbirds and summarized observations that suggested acceptance or rejection of cowbird eggs; for example, cowbirds fledging, adult orioles feeding nestling or fledgling cowbirds, or cowbird eggs that disappeared from otherwise active host clutches. Adults observed feeding a cowbird nestling or fledgling is relatively robust evidence for rearing a cowbird, but exceptions with individuals of species other than the known foster species have been reported occasionally feeding parasitic young (Sealy & Lorenzana 1997). Collectively, we used this evidence to assign a status of "response to parasitism" for each species of *Icterus*, based in part on the suggestion of Friedmann *et al.* (1977) that hosts with frequencies of parasitism recorded at more than 20% likely were accepters. We also experimentally parasitized Orchard Oriole nests at Delta Marsh, Manitoba, and recorded whether the adults accepted or rejected the introduced real or model cowbird eggs. We then discussed the patterns of acceptance and rejection throughout the genus *Icterus*.

METHODS

Status of orioles as cowbird hosts. The order and nomenclature of the species of orioles treated in this paper follow Sibley & Monroe (1990), the American Ornithologists' Union (1998, 2000) and Baker *et al.* (2003). For the following seven species of orioles there is little information on natural history, none on parasitism by cowbirds, and in some species the nest or eggs have not been described: Orange Oriole (*I. auratus*), Yellow-tailed Oriole (*I. mesomelas*), Montserrat Oriole (*I. oberi*), Bar-winged Oriole (*I. maculialatus*), Black-cowled Oriole (*I. prosthemelas*), Black-backed Oriole (*I. abeilli*), and Orange-crowned Oriole (*I.* auricapillus). Because Shiny Cowbirds apparently do not yet breed on Montserrat Island, the Montserrat Oriole remains parasitism-free (Raffaele *et al.* 1998, BirdLife International 2000, W. J. Arendt unpubl.). The breeding ranges of the other six species, however, overlap those of

the Shiny and/or Bronzed cowbird (Hilty & Brown 1986, Ridgely & Tudor 1989, Howell & Webb 1995). The nest and eggs of the Bar-winged Oriole apparently have not been described, as is also the case with the eggs of the Orange Oriole, a Yucatán endemic, and the Black-cowled Oriole of Central America (Howell *et al.* 1992, Howell & Webb 1995, Jaramillo & Burke 1999).

Experiments have confirmed acceptance or rejection for five other species of orioles, but for the other species, we summarized records of parasitism and observations that suggest acceptance or rejection of cowbird eggs. We assigned each species a status relating to its response to parasitism, based in part on the suggestion of Friedmann *et al.* (1977) that, in the absence of experimental data, a species can be assumed to be an acceptor if 20% or more of its nests are parasitized, and whether the cowbird egg is always, or nearly always, accepted, as observed by the investigator. Our categories are (1) unknown: no data or only a few isolated cases of parasitism mentioned without details in the literature; some records apparently were based on egg sets in museums or adults observed feeding fledgling cowbirds; (2) acceptance possible: frequency of parasitism less than 20% for all observed populations, possibly with records of nestling or fledgling cowbirds; (3) acceptance probable: frequency of parasitism greater than 20% or nestling or fledgling cowbirds reported; (4) acceptance or rejection possible: observations suggest a mixture of acceptance and ejection, but the level of acceptance versus ejection has not been established; and (5) acceptance or rejection confirmed: responses confirmed by experiments.

Frequency of cowbird parasitism and experimental parasitism on the Orchard Oriole. In conjunction with other studies, we located Orchard Oriole nests opportunistically from late May through early July in many years from 1977 to 2003 in the forested dune ridge that separates Lake Manitoba and Delta Marsh, Manitoba (50°11'N, 98°19'W), Canada (MacKenzie 1982; map in Sealy 1980). Orchard Orioles colonized the Delta Marsh area in the early 1970s and were first recorded nesting there in 1976 (Sealy 1980). This species now nests regularly but at low numbers in the ridge forest along the edge of Delta Marsh, but it is among the most frequently parasitized species in this host community (Sealy unpubl.).

One group of nests was inspected regularly through laying and incubation to determine parasitism frequencies, whereas at nests in the other group one real or one model cowbird egg was added to each clutch during the host's laying stage or during the first five days of incubation. Different nests were used for each experiment and the manipulations were conducted after 06:30 (CST) to avoid interfering with laying by the orioles (McMaster *et al.* in press) and were completed by 13:00. Model eggs were made of plaster-of-Paris from molds formed from real cowbird eggs collected on the study area and painted with acrylic paints and polyurethane, following Rothstein's (1975) method. Numerous tests have shown that hosts respond similarly to real and model cowbird eggs (e.g., Rothstein 1975, Hill & Sealy 1994). All nests were inspected the day after experimental parasitism and then at least every other day through five days. Following Rothstein's (1975) criteria, we considered the cowbird egg accepted if it and the host's eggs were tended by the hosts after at least five days, and ejected if the cowbird egg disappeared and the adults were in attendance. A nest was considered deserted if the contents were present, but the eggs were cold and the adults no longer attended the nest. After an experiment ended, the real or model cowbird egg was removed and examined carefully with the naked eye or with

a hand-lens for peck marks that would indicate ejection had been attempted (Rothstein 1977). Missing or damaged oriole eggs were recorded.

RESULTS

Status of oriole species as cowbird hosts

Moriche Oriole (Icterus chrysocephalus). Parasite: Shiny Cowbird; response status: unknown. Friedmann (1963) recorded a single record of parasitism by the Shiny Cowbird in Surinam.

Epaulet Oriole (Icterus cayanensis). Parasite: Shiny Cowbird; response status: unknown. In Argentina, de la Peña (1979) reported the first case of parasitism on this species, by the Shiny Cowbird, but information was insufficient to determine the response to parasitism. Fraga (2002) reported another case of parasitism on this species, based on a parasitized clutch in the Museo de La Plata that originally had been identified as belonging to the Crested Oropendola (*Psarocolius decumanus*).

Greater Antillean Oriole (Icterus dominicensis). Parasite: Shiny Cowbird; response status: acceptance confirmed. Up to 100% of nests observed of this species were parasitized by Shiny Cowbirds in Hispaniola (29.2% of 24 nests, 100% of 6 nests; Cruz *et al.* 1989) and Puerto Rico (60.7% of 28 nests, Pérez-Rivera 1986; 100% of 4 nests, Wiley 1988). Cruz *et al.* (1989) observed adult Greater Antillean Orioles feeding cowbird fledglings on Hispaniola. There was no mention of host young being fed along with the cowbirds. In Cuba, Garrido & Kirkonnell (2000) mentioned parasitism on this species by the recently arrived Shiny Cowbird. This evidence suggests acceptance and, indeed, this response was confirmed experimentally when all 7 real or model eggs introduced to nests in Puerto Rico were accepted (Cruz *et al.* 1989).

St. Lucia Oriole (Icterus laudabilis). Parasite: Shiny Cowbird; response status: unknown. This island endemic is not listed as endangered, but Keith (1997: 118) noted that "...a possible future threat is brood parasitism by the Shiny Cowbird." No parasitized nests have been recorded, although Cruz *et al.* (1989) observed one cowbird fledgling being fed by adult St. Lucia Orioles, and on three occasions, Post *et al.* (1990) observed adults feeding young cowbirds, but in all instances no young orioles. These observations suggest cowbird parasitism on the St. Lucia Oriole and acceptance of the parasite's eggs, however, until parasitism on clutches of this species has been recorded, this species' status as a cowbird host is best left as unknown.

Martinique Oriole (Icterus bonana). Parasite: Shiny Cowbird; response status: acceptance possible. Pinchon & Bon Saint-Come (1951) were the first to report parasitism by Shiny Cowbirds on Martinique Orioles. Subsequently, Bon Saint-Come reported a decline in this oriole and implicated cowbird parasitism (see Wiley 1985). If this link is borne out, this information and the observation below suggest acceptance of cowbird parasitism. During the 1986 ICBP Martinique Oriole Expedition, observations were made at a nest that contained one oriole and two Shiny Cowbird nestlings (Wood 1987). A Carib Grackle (*Quiscalus lugubris*) was observed removing one cowbird from the nest, but the oriole survived and fledged at 15 days of age. The fate of the other cowbird was not determined. Seventy-five percent of nests were reported parasitized by Shiny Cowbirds, but the number of nests examined and details are lacking (Bird Life International 2000).

Orchard Oriole (Icterus spurius). Parasites: Brown-headed Cowbird, Bronzed Cowbird; response status: acceptance confirmed for

TABLE 1. Frequency of parasitism on Orchard Oriole nests by Brown-headed and Bronzed cowbirds.

Location	Number of nests examined	Number of records	Parasitism frequency (%)	References
Oklahoma	13	6	46.2	Ely (1957)
Oklahoma	3	3	100.0	Wiens (1963)
Kansas	13	6	46.2	Platt (1975)
Kansas	15	8	53.3	Hill (1976)
North America	83	6	7.2	Friedmann et al. (1977)
Louisiana	71	20	28.2	Goertz (1977)
Kansas, Missouri, Nebraska	15	1	6.7	Lowther (1977)
Iowa	4	0	0.0	Lowther (1985)
Ontario	32	10	31.3	Peck & James (1998)
Maryland	111	5	4.5	Robbins & Blom (1996)
Nebraska	13	8	61.5	Scharf & Kren (1996)
Pennsylvania	8	2	25.0	Uhrich (1997)
Illinois	9	9	100.0	Strausberger (1998)
Illinois	12	5	42.0	Trine et al. (1998)
South Carolina	8	4	50.0	Whitehead et al. (2002)
Texas	61	1[a]	1.6[a]	K. Ellison pers. com.
Texas	61	45[b]	73.8[b]	K. Ellison pers. com.
Total[c]	471	94	20.0	

[a] Parasitism by Brown-headed Cowbirds. The single nest parasitized by Brown-headed Cowbirds was also parasitized by Bronzed Cowbirds.
[b]Parasitism by Bronzed Cowbirds.
[c]Total is for Brown-headed Cowbird parasitism only.

Brown-headed Cowbird, acceptance probable for Bronzed Cowbird. Acceptance of all Brown-headed Cowbird eggs introduced into Orchard Oriole nests in this study is consistent with the numerous records of natural parasitism on this species at several sites (Table 1). In the five studies where more than 25 nests were inspected, parasitism ranged from 2.4% (Texas) to 31.3% (Ontario). The lowest frequency of parasitism by Brown-headed Cowbirds among these studies was 1.6%, in Texas, but at this site Bronzed Cowbirds parasitized 74% of Orchard Oriole nests (Table 1). Experiments should be performed, however, to confirm the consistency of acceptance of Brown-headed Cowbird eggs among these and other populations, and also responses to the immaculate blue eggs of the Bronzed Cowbird.

Fuertes's Oriole (Icterus fuertesi). Parasite: Bronzed Cowbird; response status: acceptance possible. Of three nests of Fuertes's Oriole examined by Graber and Graber (1954: 277) on the southern coast of Tamaulipas, Mexico, one contained an oriole, in "pin feathers," plus one Bronzed Cowbird that "nearly filled the nest, although it was at about the same stage of development [as the oriole]."

Hooded Oriole (Icterus cucullatus). Parasites: Brown-headed Cowbird, Bronzed Cowbird; response status: acceptance confirmed for

Brown-headed Cowbird, acceptance probable for Bronzed Cowbird. The numerous records of parasitism by Brown-headed Cowbirds [eggs, nestlings and fledgling cowbirds (19% of 16 nests, 8% of 148 egg sets, and 71.4% of 21 nests parasitized; see Pleasants & Albano 2001)] suggest acceptance. Acceptance was confirmed experimentally in California (Friedmann *et al.* 1977) where adult Hooded Orioles, tested at about 10 nests, accepted the introduced Brown-headed Cowbird eggs (S.I. Rothstein, pers. com.). Instances of burial of cowbird eggs under new nest linings (Hardy 1970, Friedmann *et al.* 1977, J. H. Rappole & J. Klicka unpub.) have been recorded, but this behavior has not been confirmed as a response to cowbird parasitism. Hooded Orioles also are believed to be an important host of the Bronzed Cowbird (Friedmann & Kiff 1985). This is illustrated at a site in southern Texas where Brown-headed and Bronzed cowbirds co-occur during the breeding season. From 2000 to 2002, K. Ellison (pers. com.) recorded 87.2% of 86 Hooded Oriole nests parasitized by Bronzed Cowbirds, and 1.1% by the Brown-headed Cowbird, making this the most important host for the larger Bronzed Cowbird at this site.

Yellow-backed Oriole (Icterus chrysater). Parasite: Shiny Cowbird; response status: unknown. A single record of parasitism, by the Shiny Cowbird, has been recorded in Colombia (Friedmann 1963).

Yellow Oriole (Icterus nigrogularis). Probable Parasite: Shiny Cowbird; response status: rejection probable. In their comprehensive treatise of the birds of Trinidad and Tobago, Belcher & Smooker (1937) listed this species as a host of the Shiny Cowbird, but they did not provide details of parasitism. Parasitism was not detected at any of the 13 Yellow Oriole nests inspected on these Islands by Cruz *et al.* (1995). The ejection of a model cowbird egg from the single nest tested, however, suggests that if the consistency of this response is established with additional tests, then possibly some parasitism occurs in nature followed quickly by ejection of the cowbird egg.

Campo Oriole (Icterus jamacaii). Parasite: Shiny Cowbird; response status: unknown. A parasitized clutch collected in British Guiana is the only record of parasitism recorded for this species (Friedmann 1963).

Black-vented Oriole (Icterus wagleri). Parasite: Bronzed Cowbird; response status: unknown. In Mexico, Friedmann *et al.* (1977) referred to parasitism on this species at two localities, but information on parasitism frequency was insufficient to permit detection of responses to parasitism.

Troupial (Icterus icterus). Parasite: Shiny Cowbird; response status: aceptance probable. In Puerto Rico, where the Troupial was introduced, parasitism by Shiny Cowbirds has been recorded at frequencies of 61% (Pérez-Rivera 1986) to 100% (Wiley 1985). The fledging of a cowbird (Wiley 1985) also suggests acceptance. Unsubstantiated records of parasitism have been reported within this species' original range, in Guyana (Friedmann 1963) and Brazil (Sick 1993). Some Troupials re-use abandoned nests built by other species and even usurp active nests of other species, removing the nest-owners' eggs and young (Pearson 1974, Robinson 1985, Lindell 1996). Peer & Bollinger (1998) argued that nest usurpation may select for egg rejection behavior. Thus, the lack of any apparent ejection in this species is surprising.

Streaked-backed Oriole (Icterus pustulatus). Parasite: Bronzed Cowbird; response status: acceptance possible. Parasitism by Bronzed Cowbirds on this species has been reported in

Guatemala (Owen 1861), El Salvador (Dickey & van Rossem 1938; see also Thurber & Villeda 1980), and Mexico (Bailey 1906; Friedmann 1933, 1963; Russell & Monson 1998). Friedmann (1971) incorrectly reported a nest collected in Mexico containing three eggs of both the host and the Brown-headed Cowbird, despite Friedmann (1963) earlier having correctly reported the cowbird eggs as those of the Bronzed Cowbird (Friedmann & Kiff 1985). The lack of details pertaining to parasitism levels suggest only that acceptance is possible.

Jamaican Oriole (Icterus leucopteryx). Parasite: Shiny Cowbird; response status: unknown. Raffaele *et al.* (1998) have indicated parasitism on the Jamaican Oriole by the Shiny Cowbird, present in Jamaica only since 1993 (Raffaele *et al.* 1998), but details and frequency of parasitism have not been reported.

Spot-breasted Oriole (Icterus pectoralis). Parasite: Bronzed Cowbird; response status: acceptance possible. Although details are lacking, parasitism on this species by the Bronzed Cowbird has been indicated for El Salvador (Dicky & van Rossem 1938; see also Friedmann 1963), and two reports are available from Mexico (Friedmann *et al.* 1977). Spot-breasted Orioles were observed killing a Bronzed Cowbird nestling near a nest in Costa Rica, but it was not determined whether the orioles had reared the nestling (Sealy *et al.* 1998). Acceptance by these orioles would be suggested if they had reared the cowbird.

Altamira Oriole (Icterus gularis). Parasite: Bronzed Cowbird; response status: acceptance/rejection possible. Some of the confirmed records of cowbird parasitism on Altamira Orioles suggest acceptance, whereas others suggest rejection. Experiments are needed to confirm the responses of individuals to cowbird parasitism in different populations. In El Salvador, local residents informed van Rossem that this oriole was one of the most frequent hosts of the Bronzed Cowbird in the lowlands (Dickey & van Rossem 1938). Although about eight records of parasitism have been reported from Mexico (Friedmann 1963, 1971; Friedmann *et al.* 1977, Rowley 1984), parasitism on this species apparently is recorded infrequently there. Of at least 150 nests examined by T. C. Meitzen in Tamaulipas, Mexico, only two contained Bronzed Cowbird eggs (Friedmann 1963). In southern Texas, however, Oberholser (1974) stated that this oriole "does raise some cowbirds but...it appears better able [than other orioles] to survive heavy cowbird pressure." This suggests acceptance, but without qualification and no sense of the frequency of parasitism, Oberholser's observations require confirmation. Acceptance, however, is revealed by observations of Altamira Orioles feeding cowbird fledglings (Brush 1998, Hathcock 2000).

Altamira Orioles may be parasitized more frequently than the number of confirmed records suggest because some individuals may eject cowbird eggs (Hathcock 2000). Numerous authors have observed Bronzed Cowbirds visiting Altamira Oriole nests, although few have been seen entering them (Thurber & Villeda 1980, Pleasants 1981, Carter 1986, Gehlbach 1987, Brush 1998, Hathcock 2000). One nest inspected after a cowbird had entered and then left it a few seconds later had not been parasitized (Hathcock 2000). This was not surprising, as Hathcock (2000) noted, because Bronzed Cowbirds lay around sunrise (Peer & Sealy 1999), whereas the nest visits observed were later in the day. Although Hathcock (2000) recorded cowbirds visiting nests throughout the orioles' nesting cycle, significantly more nests were visited during laying than incubation.

Webster's (1962) report from the Santa Ana National Wildlife Refuge in south Texas

suggests ejection of a cowbird egg at two of 13 Altamira Oriole nests with cowbird eggshell fragments on the nest floors, plus unbroken oriole eggs. There was no evidence that any of the other 11 clutches had been parasitized. Carter (1986) found a broken cowbird egg on the ground beneath an Altamira Oriole nest that had been repeatedly entered by cowbirds, and Hathcock (2000) watched three female orioles removing Bronzed Cowbird eggs from nests apparently by puncturing the shells and then grasping the eggs in their bills. Tests of other populations are crucial to ascertain the frequency and generality of this behavior.

Audubon's Oriole (Icterus graduacauda). Parasite: Bronzed Cowbird; response status: acceptance probable. Parasitism by Bronzed Cowbirds has long been suspected to be detrimental to the reproductive success of Audubon's Oriole (Bendire 1895, Brush 2000), specifically in southern Texas where substantial numbers of Bronzed Cowbirds have colonized in the last century or more (Oberholser 1974). Implicitly, the reduced reproductive output of Audubon's Orioles reflects the destruction of clutches by Bronzed Cowbirds and rearing of nestling cowbirds at the expense of orioles. Bendire (1895: 445) noted that seven of nine clutches in the United States National Museum were parasitized with one to three cowbird eggs added to one or two oriole eggs, some of which were punctured. Other observations further suggest acceptance of cowbird eggs. Flood (1990) recorded fledgling Bronzed Cowbirds at two Audubon's Oriole nests in northeastern Tamaulipas, two from one nest and possibly more than one cowbird from the other. In 1953, the last pair of Audubon's Orioles to be recorded nesting at Santa Ana National Wildlife Refuge along the Rio Grande were observed feeding three fledged Bronzed Cowbirds (Goldman & Watson 1953). Three times, Brush (2000: 9) and others have seen Audubon's Orioles feeding 1–2 fledgling Bronzed Cowbirds along the Rio Grande, east of the Santa Ana Refuge, "where [these orioles] are still fairly common". In none of these cases were host fledglings recorded also being fed by the hosts.

Baltimore and Bullock's orioles (Icterus galbula and I. bullockii). Parasites: Brown-headed Cowbird, Bronzed Cowbird; response status: ejection confirmed for Brown-headed Cowbird, acceptance possible for Bronzed Cowbird. Results of experiments and observations of acts of parasitism have revealed conclusively that these species eject Brown-headed Cowbird eggs, often within minutes of parasitism (Rothstein 1975, 1977, 1978; Friedmann *et al.* 1977, Rohwer *et al.* 1989, Røskaft *et al.* 1993, Neudorf & Sealy 1994, Sealy & Neudorf 1995). Nevertheless, there are accounts of Brown-headed Cowbird eggs accepted and young fledging (reviewed in Friedmann *et al.* 1977, Hobson & Sealy 1987). Furthermore, Bronzed Cowbirds parasitized 22.4% of 58 nests inspected in southern Texas (K. Ellison pers. com.), which suggests that acceptance is possible for at least some eggs. However, most eggs were removed as part of a genetic study and orioles may not have had time to eject the Bronzed Cowbird eggs.

Scott's Oriole (Icterus parisorum). Parasites: Brown-headed Cowbird, Bronzed Cowbird; response status: acceptance probable for both Brown-headed Cowbirds and Bronzed Cowbirds. One report exists of the Scott's Oriole parasitized by the Brown-headed Cowbird, an apparently collected clutch containing a single cowbird egg plus three host eggs from Arizona (Friedmann & Kiff 1985). A northward expansion in recent decades has brought the Bronzed Cowbird and Scott's Oriole into sympatry and a few records of parasitism have been reported (e.g., Friedmann *et al.* 1977,

Friedmann & Kiff 1985, Russell & Monson 1998). The observations suggest acceptance in some cases, rejection in others, hence, experiments are needed to clarify the nature of these responses. The first two records offered no clues to the hosts' responses to parasitism, as both were of single clutches with one egg, in southern Arizona (Bent 1958) and Mexico Friedmann (1963). In southern Texas, Flood (2002) recorded frequencies of parasitism by Brown-headed Cowbirds of 19.3% (11 of 57 nests) and 13.7% (10 of 73 nests) in 1982 and 1983, respectively, but in 1982 this figure was 37% when the calculation included only nests initiated after cowbirds had started laying. Up to three cowbird eggs were recorded in one nest. Of eight clutches deserted during incubation, two were deserted after a cowbird egg was laid, but without controlled experiments it could not be established whether the response was to parasitism or to some other disturbance (e.g., Hill & Sealy 1994). Acceptance, however, was indicated at many other nests from which cowbirds fledged (Barlow & Flood 1988, Flood 2002).

White-edged Oriole (Icterus graceannae). Parasite: Shiny Cowbird; response status: acceptance possible. In Ecuador, Marchant (1960) recorded a nest with five nestlings, three of them Shiny Cowbirds. After the cowbirds and possibly one oriole fledged (one oriole died in the nest), an unhatched cowbird egg remained, but the fate of the other oriole nestling was not ascertained. Acceptance is suggested. Friedmann & Kiff (1985) reported two additional nests of this species parasitized, in Peru, both of which contained single Shiny Cowbird eggs.

Responses to experimental parasitism

Twenty-nine Orchard Oriole nests were experimentally parasitized, four nests with real cowbird eggs (between 1987 and 1992) and 25 nests with model cowbird eggs (2 nests in 1998, 10 in 1999, 9 in 2000, 4 in 2001). Three nests failed before the outcome of the experiment could be recorded: two were destroyed by wind (one within 24 h of parasitism, the other between 72 h and 96 h) and the third nest was depredated between 72 h and 96 h. All cowbird eggs (4 real, 22 models) were accepted at each of the other 26 nests at which full 5-day outcomes were obtained. None of the experimental nests was deserted, no cowbird eggs were pecked, and no host eggs disappeared.

Frequency of parasitism on Orchard Orioles

From 1977 to 1986, three of 12 (25%) unmanipulated nests inspected daily through egg laying and every 3–4 days during incubation were parasitized (two nests received one, the other two cowbird eggs). From 1987 to 2001, most nests found were used for experiments, but of 15 unmanipulated nests monitored during that period, six (40.0%) were parasitized, all but one with a single cowbird egg. In 2003, of seven additional unmanipulated nests inspected every 1–3 days through laying and the first half of incubation, none was parasitized. Combining all of these nests, the overall parasitism frequency from 1976 to 2003 was 26.5% (9 of 34 nests). This is only slightly higher than the overall frequency of parasitism of 20.8% for Orchard Orioles breeding at various other sites within the species' breeding range (Table 1).

Surprisingly, none of the 29 manipulated clutches was naturally parasitized. Ortega *et al.* (1994) found initial support for cowbirds avoiding already-parasitized nests and our results appear to support this idea, especially because most of our experiments were initiated during laying when parasitism was most likely to occur (see Sealy 1995). Our experiments, however, were not designed to test this hypothesis and they lacked appropriate controls. Furthermore, numerous observations

exist of cowbirds laying more than one egg per host nest (e.g., Trine 2000, McLaren *et al.* 2003), including in Orchard Oriole nests (Scharf & Kren 1996, this study). These eggs may be laid by the same or different female cowbirds (McLaren *et al.* 2003). Our results, therefore, provide only suggestive evidence that cowbirds avoided the already-parasitized Orchard Oriole nests.

Cowbirds fledged from the five naturally parasitized nests inspected through fledging (one young fledged from four nests and two from the fifth). One fledgling cowbird was observed being fed by an adult male Orchard Oriole on 7 July 1994. Neither the female oriole nor any oriole fledglings were observed, but because brood division has been observed in this species (Sealy 1980), the female and young may have been elsewhere.

To recapitulate, the results of simulated cowbird parasitism on nests of five of the 29 species of orioles revealed that three or possibly four species eject the foreign eggs, whereas one species accepts them. Our experiments on the Orchard Oriole resulted in acceptance of real and model cowbird eggs at all 29 nests tested, which, coupled with high frequencies of parasitism recorded for many other populations of Orchard Orioles, confirms the Orchard Oriole as an accepter. The breeding biology of seven species of orioles is little known, but the information available on cowbird parasitism for 16 other species suggests acceptance is possible or probable for 15 and ejection is possible for at least one additional species. Both accepters and rejecters occurred among the orioles, but the evidence suggests most species accept cowbird eggs.

DISCUSSION

Responses by Orchard Orioles and other orioles to cowbird parasitism. Experimental parasitism has revealed that Baltimore Orioles, Bullock's Orioles, and Yellow Orioles (only one nest tested) eject cowbird eggs, whereas Orchard Orioles, Hooded Orioles, and Black-cowled Orioles are accepters. Published observations of acceptance of cowbird eggs, fledged cowbirds and fledglings fed by hosts, however, are sufficient to suggest possible or probable acceptance by eight other species of orioles. Cowbirds fledged from Altamira Oriole nests certainly reveals acceptance by some individuals, but cowbird eggs found on the ground under nests (Hathcock 2000) suggests ejection, although these eggs may have knocked over the side of the nest during failed parasitism attempts (K. Ellison pers. com.). Again, experiments must be conducted to confirm these responses and to determine whether all individuals in the populations consistently accept or reject parasitism. However, it may be too late to conduct these experiments on threatened and endangered species.

Investigations of several species of orioles have led investigators to suspect or even blame the declines of some species or populations on the reduced productivity wrought by cowbird parasitism (e.g., Oberholser 1974, Pérez Rivera 1978, Carter 1986, Brush 1998, Flood 1990; see also Wiley 1985). However, a link between cowbird parasitism and these declines has not been made for any species. If real, however, acceptance by all or most individuals in these populations certainly would be indicated. Knowledge of the frequency of cowbird parasitism on species and the responses of hosts to parasitism have conservation implications because a high frequency of parasitism, especially on small populations of hosts that accept parasitism, may compromise their reproductive success (see Post & Wiley 1976). Ejection eliminates parasitism, therefore, the frequency of parasitism on certain species may be under-recorded and, hence, clutch sizes may be reduced by the activities of parasites at host nests (e.g., Sealy

1992) that investigators may attribute to something other than parasitism.

We urge workers throughout Central America, South America and the Caribbean area to study the breeding biology of orioles and to obtain information on the frequency of cowbird parasitism and, where there are sufficient numbers of nests, experimentally parasitize them to determine the responses of adults to cowbird parasitism. We appreciate that experiments cannot be conducted on threatened or endangered species or populations and that nests of many species of orioles are difficult to reach for study. In many regions, range expansions are bringing cowbirds into contact with new host populations and species. Experiments should be conducted on species whose breeding ranges overlap or do not yet overlap with cowbird ranges. The expansion of the Brown-headed Cowbird in North America in the past 200 years has been well documented (Mayfield 1965, Rothstein 1994, Ortega 1998), as has the rapidly expanding range of the Shiny Cowbirds throughout most of the Greater Antilles and Lesser Antilles to the southeastern United States, and also in parts of South America (Post & Wiley 1977, Cruz *et al.* 1985, Høgsås 1999, Marín 2000). It is probably only a matter of time before Shiny Cowbirds reach the Yucatán of Mexico and other areas of Central America where orioles (Howell *et al.* 1992) and other potential host species will be vulnerable to parasitism (Kluza 1998), both within and outside areas already occupied by the Bronzed Cowbird. Knowledge of a species' response to parasitism should help focus conservation efforts on those species most vulnerable to parasitism, that is, species that accept parasitism.

Acceptance and rejection among the species of Icterus. Focusing on the New World orioles of the genus *Icterus*, we found that among the five species previously tested experimentally, the results revealed a mixture of responses: two species accepted cowbird parasitism, whereas the other three rejected it (although for one species only a single nest was tested). These results are clear-cut, but anecdotal observations summarized for many of the other species also suggests there are additional accepters and possibly also rejecters within this genus. On the surface, it appears that these results do not support Rothstein's hypothesis, but in his original paper, Rothstein (1975) did not specify what he meant by "taxon," although his discussion centered on the genus. With more data available, Peer & Sealy (in press) found a correlation between rejection behavior and taxonomic affiliation in hosts of the Brown-headed Cowbird, which suggests that once rejection behavior evolves, it may be maintained.

Recent use of molecular genetic techniques has revealed three groups of species within *Icterus* (Omland *et al.* 1999). Omland *et al.* (1999) confirmed the monophyly of the genus *Icterus* and determined that the genus consists of three major clades. It is interesting to note the known or suspected response to cowbird parasitism for each species within the clades. All three species of orioles confirmed experimentally as accepters, as well as two possible accepters, are grouped in clade A; the responses of the other species in this clade are unknown. Clade B contains one probable and two possible accepters and the responses of the other species are unknown, whereas the confirmed and possible ejecters are all in clade C. Also in the latter clade are three species of probable and possible accepters, two species whose responses are unknown and one for which there is no information. Thus, there is among these clades some support for Rothstein's hypothesis, but apparently with a few exceptions. Nevertheless, most oriole species remain to be tested before their responses to cowbird parasitism can be determined or confirmed. This will be accom-

plished only by testing adequate numbers of nests for each species and we urge workers to conduct these experiments.

ACKNOWLEDGMENTS

We thank the staff of the Delta Marsh Field Station (University of Manitoba) for providing accommodations during the field work on Orchard Orioles. Officers of the Delta Waterfowl Research Station and Portage Country Club permitted us to conduct some of this work on their properties. Celia McLaren, Glen McMaster, Kevin Shonk, Becky Stewart, and Robyn Underwood found some of the nests. Wayne J. Arendt kindly provided a copy of his unpublished report on the status of the Montserrat Oriole, prepared for the Government of Montserrat. Kevin Ellison provided unpublished data on cowbird parasitism on orioles in south Texas and commented on a draft of the manuscript. The reviewers, M. Marín and J. W. Wiley, commented constructively on the manuscript. This study was supported by a grant from the Natural Sciences and Engineering Research Council of Canada to S. G. Sealy and a University of Manitoba Graduate Fellowship to T. J. Underwood.

REFERENCES

American Ornithologists' Union. 1998. Check-list of North American birds. 7th ed. American Ornithologists' Union, Washington, D.C.

American Ornithologists' Union. 2000. Forty-second supplement to the American Ornithologists' Union check-list of North American birds. Auk 117: 847–858.

Bailey, H. H. 1906. Ornithological notes from western Mexico and the Tres Marias and Isla-Bella Islands. Auk 23: 369–391.

Baker, J. M., E. López-Medrano, A. G. Navarro-Sigüenza, O. R. Rojas-Soto, & K. E. Omland. 2003. Recent speciation in the Orchard Oriole group: divergence of *Icterus spurius spurius* and *Icterus spurius feurtesi*. Auk 120: 848–859.

Barlow, J. C., & N. J. Flood. 1988. Factors influencing bird population dynamics in the northern Chihuahuan Desert. Pp. 81–88 *in* Powell, M. (ed.). Third symposium on resources of the Chihuahuan Desert – U.S. and Mexico. Chihuahuan Desert Research Institute, Alpine, Texas.

Belcher, C., & G. D. Smooker. 1937. Birds of the colony of Trinidad and Tobago–Part VI. Ibis, ser. 14, 79: 504–550.

Bendire, C. 1895. Life histories of North American birds, from parrots to grackles. Special Bulletin, No. 3, U.S. National Museum, Washington, D.C.

Bent, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Nat. Mus. Bull. 211: 1–549.

BirdLife International. 2000. Threatened birds of the world. Lynx Edicions and BirdLife International, Barcelona, Spain, and Cambridge, UK.

Boggs, G. O. 1961. Notas sobre las aves de 'El Centro' en el valle medio del Rio Magdalena-Colombia. Noved. Colomb. 1: 401–423.

Briskie, J. V., & S. G. Sealy. 1987. Responses of Least Flycatchers to experimental inter- and intraspecific brood parasitism. Condor 89: 899–901.

Brush, T. 1998. A closer look: Altamira Oriole. Birding 30: 46–53.

Brush, T. 2000. Audubon's Oriole. Texas Birds 2(5): 5–9.

Carter, M. D. 1986. The parasitic behavior of the Bronzed Cowbird in south Texas. Condor 88: 11–25.

Cruz, A., T. H. Manolis, & R. W. Andrews. 1995. History of Shiny Cowbird *Molothrus bonariensis* brood parasitism in Trinidad and Tobago. Ibis 137: 317–321.

Cruz, A., T. Manolis, & J. W. Wiley. 1985. The Shiny Cowbird: a brood parasite expanding its range in the Caribbean region. Ornithol. Monogr. 36: 607–620.

Cruz, A., J. W. Wiley, T. K. Nakamura, & W. Post. 1989. The Shiny Cowbird *Molothrus bonariensis* in the West Indian region – Biogeographical and ecological implications. Pp. 519–540 *in* Wood, C. A. (ed.). Biogeography of the West Indies: past, present, and future. Sandhill Crane Press, Gainesville, Florida.

Curson, D. R., C. B. Goguen, & N. E. Matthews. 1998. Western Wood-Pewees accept cowbird eggs. Great Basin Nat. 58: 90–91.

de la Peña, M. R. 1979. Parasitismo en aves (2ª Parte). CYTA 10: 11–16.

Dickey, D. R., & A. J. van Rossem. 1938. The birds of El Salvador. Field Museum of Natural History, Publication 406, Zoological Series 23, Chicago, Illinois.

Ely, C. A. 1957. Comparative nesting success of certain south-central Oklahoma birds. M.S. thesis, Univ. of Oklahoma, Norman, Oklahoma.

Finch, D. M. 1982. Rejection of cowbird eggs by Crissal Thrashers. Auk 99: 719–724.

Flood, N. J. 1990. Aspects of the breeding biology of Audubon's Oriole. J. Field Ornithol. 61:290–302.

Flood, N. J. 2002. Scott's Oriole (*Icterus parisorum*). *In* Poole, A., & F. Gill (eds.). The birds of North America, No. 608. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C.

Fraga, R. M. 1985. Host-parasite interactions between Chalk-browed Mockingbirds and Shiny Cowbirds. Ornithol. Monogr. 36: 829–844.

Fraga, R. M. 2002. Notes on new or rarely reported Shiny Cowbird hosts from Argentina. J. Field Ornithol. 73: 213–219.

Friedmann, H. 1929. The cowbirds: a study in the biology of social parasitism. C.C. Thomas, Springfield, Illinois.

Friedmann, H. 1933. Further notes on the birds parasitized by the Red-eyed Cowbird. Condor 35: 189–191.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. Nat. Mus. Bull. 233: 1–276.

Friedmann, H. 1971. Further information on the host relations of the parasitic cowbirds. Auk 88: 239–255.

Friedmann, H., & L. F. Kiff. 1985. The parasitic cowbirds and their hosts. Proc. West. Found. Vertebr. Zool. 2: 226–302.

Friedmann, H., L. F. Kiff, & S. I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithson. Contrib. Zool. 235: 1–75.

Garrido, O., & A. Kirkonnell. 2000. Field guide to the birds of Cuba. Comstock, Ithaca, New York.

Gelhbach, F. R. 1987. Natural history sketches, densities, and biomass of breeding birds in evergreen forests of the Rio Grande, Texas, and Rio Corona, Tamaulipas, Mexico. Texas J. Sci. 39: 241–251.

Goertz, J. W. 1977. Additional records of Brown-headed Cowbird nest parasitism in Louisiana. Auk 94: 386–389.

Goldman, L. C., & F. G. Watson. 1953. South Texas region. Audubon Field Notes 7: 316–320.

Graber, R. R., & J. W. Graber. 1954. Comparative notes on Fuertes and Orchard orioles. Condor 56: 274–282.

Haas, C A., & K. H. Haas. 1998. Brood parasitism by Brown-headed Cowbirds on Brown Thrashers: frequency and rates of rejection. Condor 100: 535–540.

Hardy, J. W. 1970. Duplex nest construction by Hooded Oriole circumvents cowbird parasitism. Condor 72: 491.

Hathcock, C. R. 2000. Factors affecting reproductive success in hosts of the Bronzed Cowbird (*Molothrus aeneus*) in the Rio Grande Valley, Texas. M.S. thesis, Univ. of Texas-Pan American, Edinberg, Texas.

Hill, D. P., & S. G. Sealy. 1994. Desertion of nests parasitized by cowbirds: have Clay-coloured Sparrows evoled an anti-parasite defence? Anim. Behav. 48: 1063–1070.

Hill, R. A. 1976. Host-parasite relationships of the Brown-headed Cowbird in a prairie habitat of west-central Kansas. Wilson Bull. 88: 555–565.

Hilty, S. L., & W. L. Brown. 1986. A guide to the birds of Colombia. Princeton Univ. Press, Princeton, New Jersey.

Hobson, K. A., & S. G. Sealy. 1987. Cowbird egg buried by a Northern Oriole. J. Field Ornithol. 58: 222–224.

Høgsås, T. E., E. M. Arenas, & C. Collado. 1999, Tordo parasítico avanzando en al sur del Perú. Cotinga 12: 76.

Howell, S. N. G., S. Webb, & B. M. de Montes. 1992. Colonial nesting of the Orange Oriole. Wilson Bull. 104: 189–190.

Howell, S. N. G., & S. Webb. 1995. A guide to the

birds of Mexico and northern Central America. Oxford Univ. Press, Oxford, UK.

Jaramillo, A., & P. Burke. 1999. New World blackbirds, the icterids. Princeton Univ. Press, Princeton, New Jersey.

Keith, A. R. 1997. The birds of St. Lucia. B.O.U. Check-list, No. 15, British Ornithologists' Union, Tring, UK.

Kluza, D. A. 1998. First record of Shiny Cowbird (*Molothrus bonariensis*) in Yucatán, Mexico. Wilson Bull. 110: 429–430.

Lindell, C. 1996. Benefits and costs to Plain-fronted Thornbirds (*Phacellodomus rufifrons*) of interactions with avian nest associates. Auk 113: 565–577.

Lowther, P. E. 1977. Old cowbird breeding records from the Great Plains region. Bird-Banding 48: 358–369.

Lowther, P. E. 1985. Catalog of Brown-headed Cowbird hosts from Iowa. Proc. Iowa Acad. Sci. 92: 95–99.

McLaren, C. M., B. E. Woolfenden, H. L. Gibbs, & S. G. Sealy. 2003. Genetic and temporal patterns of multiple parasitism by Brown-headed Cowbirds (*Molothrus ater*) on Song Sparrows (*Melospiza melodia*). Can. J. Zool. 81: 281–286.

McMaster D. G., D. L, Neudorf, S. G. Sealy, & T. E. Pitcher. In press. A comparative analysis of laying times in passerine birds. J. Field Ornithol.

MacKenzie, D. I. 1982. The dune-ridge forest, Delta Marsh, Manitoba: overstory vegetation and soil patterns. Can. Field-Nat. 96: 61–68.

Marchant, S. 1960. The breeding of some S.W. Ecuadorian birds. Ibis 102: 584–599.

Marín, M. 2000. The Shiny Cowbird (*Molothrus bonariensis*) in Chile: introduction or dispersion? Its hosts and parasitism trends. Ornitol. Neotrop. 11: 285–296.

Mayfield, H. F. 1965. The Brown-headed Cowbird, with old and new hosts. Living Bird 4: 13–28.

McLaren, C. M., B. E. Woolfenden, H. L. Gibbs, & S. G. Sealy. 2003. Genetic and temporal patterns of multiple parasitism by Brown-headed Cowbirds (*Molothrus ater*) on Song Sparrows (*Melospiza melodia*). Can. J. Zool. 81: 281–286.

Neudorf, D. L., & S. G. Sealy. 1994. Sunrise nest attentiveness in cowbird hosts. Condor 96: 162–169.

Oberholser, C. H. 1974. The bird life of Texas. Volume 2. Univ. of Texas Press, Austin, Texas.

Omland, K. E., S. M. Lanyon, & S. J. J. Fritz. 1999. A molecular phylogeny of the New World orioles (*Icterus*): the importance of dense taxon sampling. Mol. Phylogenet. Evol. 12: 224–239.

Ortega, C. P. 1998. Cowbirds and other brood parasites. Univ. of Arizona Press, Tucson, Arizona.

Ortega, C. P., J. C. Ortega, & A. Cruz 1994. Use of artificial Brown-headed Cowbird eggs as a potential management tool in deterring parasitism. J. Wildl. Manage. 58: 488–492.

Owen, R. 1861. On the nesting of some Guatemalan birds. Ibis 1861: 58–69.

Pearson, D. L. 1974. Use of abandoned cacique nests by nesting Troupials (*Icterus icterus*): precursor to parasitism? Wilson Bull. 86: 290–291.

Peck, G. K., & R. D. James. 1998. Breeding birds of Ontario: nidiology and distribution. Volume 2: Passerines (First revision – Part C: tanagers to Old World sparrows). Ontario Birds 16: 111–127.

Peer, B. D., & E. K. Bollinger. 1998. Rejection of cowbird eggs by Mourning Doves: a manifestation of nest usurpation? Auk 115: 1057–1062.

Peer, B. D., & S. G. Sealy. 1999. Laying time of the Bronzed Cowbird. Wilson Bull. 111: 137–139.

Peer, B. D., & S. G. Sealy. 2000. Responses of Scissor-tailed Flycatchers (*Tyrannus forficatus*) to experimental cowbird parasitism. Bird Behav. 13: 63–67.

Peer, B. D., & S. G. Sealy. In press. Correlates of egg ejection behavior in hosts of the Brown-headed Cowbird. Condor.

Peer, B. D., K. S. Ellison, & S. G. Sealy. 2002. Intermediate frequencies of egg ejection by Northern Mockingbirds (*Mimus polyglottos*) sympatric with two cowbird species. Auk 119: 855–858.

Pérez Rivera, R. A. 1978. Notas sobre los Icteridos vulnerables en peligro de extincion en Puerto Rico. Sci. Cienc. 5: 70–74.

Pérez-Rivera, R. A. 1986. Parasitism by the Shiny Cowbird in the interior part of Puerto Rico. J. Field Ornithol. 57: 99–104.

Pinchon, R., & M. Bon Saint-Come. 1951. Notes et observations sur les oiseaux des Antilles Françaises. Oiseau Rev. Fr. Ornithol. 21: 229–277.

Platt, D. R. 1975. Breeding birds of Sand Prairie Natural History Reservation, Harvey County,

Kansas. Am. Birds 29: 1146–1151.

Pleasants, B. Y. 1981. Aspects of the breeding biology of a subtropical oriole, *Icterus gularis*. Wilson Bull. 93: 531–537.

Pleasants, B. Y., & D. J. Albano. 2001. Hooded Oriole *Icterus cucullatus*. *In* Poole, A., & F. Gill (eds.). The birds of North America, No. 568. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C.

Post, W., & J. W. Wiley. 1976. The Yellow-shouldered Blackbird–present and future. Am. Birds 30: 13–20.

Post, W., & J. W. Wiley. 1977. Reproductive interactions of the Shiny Cowbird and the Yellow-shouldered Blackbird. Condor 79: 176–184.

Post, W., T. K. Nakamura, & A. Cruz. 1990. Patterns of Shiny Cowbird parasitism in St. Lucia and southwestern Puerto Rico. Condor 92: 461–469.

Raffaele, H., J. Wiley, O. Garrido, A. Keith, & J. Raffaele. 1998. A guide to the birds of the West Indies. Princeton Univ. Press, Princeton, New Jersey.

Rich, T. D., & S. I. Rothstein. 1985. Sage Thrashers reject cowbird eggs. Condor 87: 561–562.

Ridgely, R. S., & G. Tudor. 1989. The birds of South America. Volume 1. The oscine passerines. Univ. of Texas Press, Austin, Texas.

Robbins, C. S., & A. T. Blom. 1996. Atlas of the breeding birds of Maryland and the District of Columbia. Univ. of Pittsburgh Press, Pittsburgh, Pennsylvania.

Robinson, S. K. 1985. The Yellow-rumped Cacique and its associated nest pirates. Ornithol. Monogr. 36: 898–907.

Rohwer, S., C. D. Spaw, & E. Røskaft. 1989. Costs to Northern Orioles of puncture-ejecting parasitic cowbird eggs from their nests. Auk 106: 734–738.

Røskaft, E., S. Rohwer, & C. D. Spaw. 1993. Cost of puncture ejection compared with costs of rearing cowbird chicks for Northern Orioles. Ornis Scand. 24: 28–32.

Rothstein, S. I. 1971. Observation and experiment in the analysis of interactions between brood parasites and their hosts. Am. Nat. 105: 71–74.

Rothstein, S. I. 1974. Mechanisms of avian egg recognition: possible learned and innate factors. Auk 91: 796–807.

Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250–271.

Rothstein, S. I. 1976. Experiments on defenses Cedar Waxwings use against cowbird parasitism. Auk 93: 675–691.

Rothstein, S. I. 1977. Cowbird parasitism and egg recognition of the Northern Oriole. Wilson Bull. 89: 21–32.

Rothstein, S. I. 1978. Mechanisms of avian egg-recognition: additional evidence for learned components. Anim. Behav. 26: 671–677.

Rothstein, S. I. 1982. Mechanisms of avian egg recognition: which egg parameters elicit responses by rejecter species? Behav. Ecol. Sociobiol. 11: 229–239.

Rothstein, S. I. 1986. A test of optimality: egg recognition in the Eastern Phoebe. Anim. Behav. 34: 1109–1119.

Rothstein, S. I. 1994. The cowbird's invasion of the far west: history, causes and consequences experienced by host species. Stud. Avian Biol. 15: 301–315.

Rowley, J. S. 1984. Breeding records of land birds in Oaxaca, Mexico. Proc. West. Found. Vertebr. Zool. 2: 76–224.

Russell, S. M., & G. Monson. 1998. The birds of Sonora. Univ. of Arizona Press, Tucson, Arizona.

Scharf, W. C., & J. Kren. 1996. Orchard Oriole (*Icterus spurius*). *In* Poole, A., & F. Gill (eds.). The birds of North America, No. 255. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C.

Scott, D. M. 1977. Cowbird parasitism on the Gray Catbird at London, Ontario. Auk 94: 18–27.

Sealy, S. G. 1980. Breeding biology of Orchard Orioles in a new population in Manitoba. Can. Field-Nat. 94: 154–158.

Sealy, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. Condor 94:40–54.

Sealy, S. G. 1995. Burial of cowbird eggs by parasitized Yellow Warblers: an empirical and experimental study. Anim. Behav. 49: 877–889.

Sealy, S. G., & R. C. Bazin. 1995. Low frequency of observed cowbird parasitism on Eastern King-

birds: host ejection, effective nest defense, or parasite avoidance. Behav. Ecol. 6: 140–145.

Sealy, S. G., & D. L. Neudorf. 1995. Male Northern Orioles eject cowbird eggs: implications for the evolution of rejection behavior. Condor 97: 369–375.

Sealy, S. G., & J. C. Lorenzana. 1997. Feeding of nestling and fledgling brood parasites by individuals other than the foster parents: a review. Can. J. Zool. 75: 1739–1752.

Sealy, S. G., J. E. Sánchez, R. G. Campos, & A. Marin. 1998. Bronzed Cowbird hosts: new records, trends in host use, and cost of parasitism. Ornitol. Neotrop. 8: 175–184.

Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, New Haven, Connecticut.

Sick, H. 1993. Birds in Brazil. Princeton Univ. Press, Princeton, New Jersey.

Skutch, A. F. 1996. Orioles, blackbirds, and their kin. Univ. of Arizona Press, Tucson, Arizona.

Strausberger, B. M. 1998. Temporal patterns of host availability, Brown-headed Cowbird brood parasitism, and parasite egg mass. Oecologia 116: 267–274.

Thurber, W. A., & A. Villeda. 1980. Notes on parasitism by Bronzed Cowbirds in El Salvador. Wilson Bull. 92: 112–113.

Trine, C. L. 2000. Effects of multiple parasitism on cowbird and Wood Thrush nesting success. Pp. 135–144 *in* Smith, J. N. M., T. L. Cook, S. I. Rothstein, S. K. Robinson, & S. G. Sealy (eds.). Ecology and management of cowbirds and their hosts. Univ. of Texas Press, Austin, Texas.

Trine, C. L., W. D. Robinson, & S. K. Robinson. 1998. Consequences of Brown-headed Cowbird brood parasitism for host population dynamics. Pp. 273–295 *in* Rothstein, S. I., & S. K. Robinson (eds.). Parasitic birds and their hosts. Oxford Univ. Press, Oxford, UK.

Uhrich, W. D. 1997. A century of bird life in Berks County, Pennsylvania. Reading Public Museum, Reading, Pennsylvania.

Underwood, T. J., S. G. Sealy, & C. M. McLaren. In press. Eastern Wood-Pewees as Brown-headed Cowbird hosts: accepters but infrequently parasitized. J. Field Ornithol.

Webster, F. S., Jr. 1962. South Texas region. Audubon Field Notes 16: 489–493.

Whitehead, M. A., S. H. Schweitzer, & W. Post. 2002. Cowbird/host interactions in a southeastern old-field: a recent contact area? J. Field Ornithol. 73: 379–386.

Wiens, J. A. 1963. Aspects of cowbird parasitism in southern Oklahoma. Wilson Bull. 75: 130–139.

Wiley, J. W. 1985. Bird conservation in the United States Caribbean. Bird Conserv. 2: 107–159.

Wiley, J. W. 1988. Host selection by the Shiny Cowbird. Condor 90: 289–303.

Wood, P. 1987. Report of the 1986 Univ. of East Anglia Martinique Oriole expedition. ICBP Study Rept. No. 23, Cambridge, UK.