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RESPONSES OF POTENTIAL HOST SPECIES TO SIMULATED BRONZED COWBIRD (*MOLOTHRUS AENEUS*) PARASITISM AT TWO SITES IN COSTA RICA

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Abstract · To assign responses of acceptance and rejection of potential hosts to parasitism by the Bronzed Cowbird (*Molothrus aeneus*) in Costa Rica, I performed 110 egg manipulations at nests of 17 known and potential host species. Ten responses by three species were scored as ejections (*Pitangus sulphuratus*, *Cyclarhis gujanensis*, *Turdus grayi*) and three species deserted their nests (*Zonotrichia capensis*, *Arremenops conirostris, Piranga bidentata*). None of the artificial eggs removed from nests at which they were accepted were pecked, which would indicate attempted ejection. Additional experiments are necessary to determine whether mixed responses of acceptance and rejection by individuals of the same species are more common in tropical environments.

Resumen · Respuestas de especies hospederas potenciales al parasitismo simulado del tordo ojirrojo (*Molothrus aeneus*) en dos sitios en Costa Rica
Para determinar las respuestas de aceptación o rechazo por parte de potenciales hospederos de parasitismo de cría del tordo ojirrojo (*Molothrus aeneus*) en Costa Rica, hice 110 manipulaciones de huevos en los nidos de 17 especies hospederas comprobadas o potenciales. 10 respuestas en tres especies fueron determinadas como expulsiones (*Pitangus sulphuratus*, *Cyclarhis gujanensis*, *Turdus grayi*) y tres especies abandonaron sus nidos (*Zonotrichia capensis*, *Arremenops conirostris, Piranga bidentata*). Ninguno de los huevos artificiales removidos de los nidos en donde fueron aceptados presentaron signos de intentos de expulsión. Experimentos adicionales son necesarios para determinar si las respuestas mixtas de aceptación y rechazo por parte de individuos de una misma especie son más comunes en ambientes tropicales.

Key words: Acceptance · Brood parasitism · Clutch manipulation · Desertion · Ejection

INTRODUCTION

Hosts of the parasitic Brown-headed Cowbird (*Molothrus ater*) generally accept or reject cowbird eggs, depending on their ability to discriminate and eject foreign eggs from their nests (Rothstein 1975, Peer & Sealy 2004). Hosts used and their response to parasitism by the generalist Bronzed Cowbird (*M. aeneus*) are incompletely known. This brood parasite ranges from extreme southwestern and central United States to northern Colombia (Ellison & Lowther 2020). In Costa Rica, 19 species are known to have been parasitized by the Bronzed Cowbird (Sealy et al. 1997), but whether these and other potential host species accept or reject the cowbird's egg has been determined experimentally only for the Clay-colored Thrush (*Turdus grayi*) (Rasmussen et al. 2012). Results of experimental clutch manipulations at nests of species of some known and potential hosts in Costa Rica are reported in the present study, which further our understanding of coevolution in brood-parasitic systems.

METHODS

Study sites. Nests were tested at two sites in Costa Rica at the end of the dry season. 1) Property of La Selva Biological Station (10°25' N, 84°59' W), ~35 a.s.l., in the Caribbean lowlands adjacent to Braulio Carrillo National Park, near the town of Puerto Viejo de Sarapiquí, Province of Heredia. This site was characterized as tropical lowland rainforest, with species-rich, multilayered communities of primary forest. The experiment was conducted from 26 to 31 March 1997 on abandoned pastures and plantations in various stages of succession, and selectively logged secondary forest. 2) Vicinity of El Copey de Dota (9°39' N, 83° 55' W) and Santa Maria de Dota (9°39'N, 83°58''W), approximately 25 km south of Cartago on the Pacific slope of the Talamanca mountain range, at c. 1850 m a.s.l. Habitat varied between large apple orchards, cloud forests, cattle pastures, pastures and native forests dominated by oak (*Quercus* spp.). Low-lying and riparian areas tended to be used by humans, whereas higher elevation sites remained as cloud forest. Experimental parasitism was conducted from 22 March to 13 April 1999, 17 March to 9 April 2007, and 4 April to 27 April 2008 at El Copey de Dota. Five nests were tested between 7 and 19 April 2008 at Santa

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Table 1. Responses of 17 species of known and potential hosts of the Bronzed Cowbird (*Molothrus aeneus*) to parasitism, simulated by introduction of a single artificial cowbird egg into each nest. [a] Tests conducted at La Selva Biological Station. [b] Tests conducted at El Copey/Santa Maria. [c] Ejected on day 2, nest deserted two days later. [d] Acceptance at one nest through day 4. [e] All ejections occurred within 24 hours of parasitism. [f] Artificial egg inserted into one nest one day before young hatched. [g] Nest deserted by day 3. [h] Artificial egg accepted for at least 2 days (2nd host egg laid after nest inspected on day 2; by day 3, nest depredated).

Species	# nests tested	# accepted	# ejected	# deserted	# depredated
Pitangus sulphuratus[a,b]	2	1	1[c]	–	–
Myiozetetes granadensis[a]	2	2[d]	–	–	–
Tyrannus melancholicus[b]	7	7	–	–	–
Empidonax flavescens[b]	2	2	–	–	–
Sayornis nigricans[b]	3	3	–	–	–
Cyclarhis gujanensis[b]	1	–	1[e]	–	–
Cantorchilus modestus[a]	1	1	–	–	–
Turdus grayi[a,b]	52	38	8[e]	–	6
Zonotrichia capensis[b]	21[f]	14	–	4	2
Chlorospingus flavopectus[b]	1	1	–	–	–
Arremonops conirostris[a]	1	–	–	1[g]	–
Atlapetes albinucha[b]	2	1	–	–	1[h]
Piranga bidentata[b]	4	3	–	1	–
Rhamphocelus passerinii[a]	6	6	–	–	–
Thraupis episcopus[a,b]	1	1	–	–	–
Thraupis palmarum[b]	2	2	–	–	–
Saltator maximus[a]	2	1	–	–	1

Maria de Dota.

Experimental parasitism. Artificial eggs were constructed out of plaster-of-Paris, with cores of polystyrene foam to reduce weight, and painted and polished to simulate the light bluish-green and texture of Bronzed Cowbird eggs, respectively (Ellison & Lowther 2009). A subsample of artificial eggs used in this experiment averaged (mean ± SD) 23.8 ± 0.5 mm by 18.3 ± 0.2 mm (N = 58), and weighed 4.8 ± 0.4 g (N = 49). Eggs of nominate *aeneus* averaged 23.6 mm (range 21.4-25.2) by 18.4 mm (range 17.4-19.4, N = 23), and averaged 3.91 g, N = 61 (Ellison & Lowther 2009).

I introduced artificial Bronzed Cowbird eggs into nests located opportunistically, which contained one or more eggs during the laying or incubation stages. I inspected them daily for three days at La Selva and five days at El Copey to record whether the potential hosts accepted or ejected the artificial cowbird egg. Nests deserted following addition of artificial eggs were recorded as rejected, but this response was unconfirmed due to lack of appropriate controls. Following Rothstein's (1975) criteria, I recorded an artificial egg as accepted if it remained undamaged in the nest with its host eggs, and ejected if the artificial egg went missing from active nests. I removed the artificial egg from nests at which it had been accepted and examined it for peck marks that indicated ejection had been attempted (Rothstein 1977). In species previously tested (Rothstein 1975, Lorenzana & Sealy 2001), less than 1% of ejections occur after five days. Therefore, eggs accepted for five days are likely to also remain accepted through the remainder of the nesting attempt. Nests were considered depredated if all host eggs were gone or were damaged during the 5-day test period.

RESULTS AND DISCUSSION

Response to artificial eggs. Of 110 experimental egg manipulations performed at nests of 17 known and potential host species, 10 responses were scored as ejection (three species), six nests were deserted (four species), and 10 nests were depredated before a response could be assigned (Table 1). Nine of 10 ejections occurred within 24 hours of parasitism, whereas the artificial egg was ejected at the other nest two days after parasitism. None of the artificial eggs removed from nests following acceptance had discernible peck marks that would indicate that ejection by puncture had been attempted. Natural parasitism was not recorded at any of the nests tested in this experiment, although Bronzed Cowbirds were observed on at least three days during the test periods. Below, the status of each species as a potential known host of the Bronzed Cowbird and other cowbird species is summarized, as well as responses to parasitism based on observations and tests conducted in other parts of the host species' range.

Great Kiskadee (*Pitangus sulphuratus*). Owen (1861: 61-62) referred to this species as a host in Guatemala, stating that"… the eggs are found … occasionally [in the nest] of the largest species of 'Chitillo' [Great Kiskadee]." Friedmann (1929, 1963), also without details, listed this species as a host in Guatemala and in Argentina. Despite the suggested inaccessibility of the domed nests to cowbirds (Carter 1986) and aggressive nest defense (Gorena 1995), parasitism has been recorded by the Shiny Cowbird (*Molothrus bonariensis*) in Argentina (Wilson 1979, Contreras 1980), which includes fledgling cowbirds fed by the putative hosts (Friedmann & Kiff 1985, Mason 1986). In an experiment conducted in Argentina, this species removed all Shiny Cowbird eggs of the immaculate morph, but only half of the eggs of the spotted morph. Nevertheless, Mason (1986) did not assign acceptor or ejector status because of the small sample sizes (four nests, each "parasitized" with immaculate and spotted eggs). That the immaculate egg of the Bronzed Cowbird was removed from one nest in the present experiment (Table 1) reveals the need for further tests to determine the nature of its response to parasitism.

Gray-capped Flycatcher (*Myiozetetes granadensis*). There are no records of cowbird parasitism for this species.

Tropical Kingbird (*Tyrannus melancholicus*). Acceptance of artificial eggs accords with the dozen or so records of parasitism on this species by the Shiny Cowbird in Argentina (Friedmann 1929, Friedmann et al. 1977, Friedmann & Kiff 1985), which include two instances of young reared by this

species (Fraga 1978). An additional experiment is required to determine whether acceptance is the prevalent response in this and other species of *Tyrannus* that nest in the tropics (also see Mason 1986), as cowbird eggs are ejected by temperate-nesting species of *Tyrannus* (Rothstein 1975, Rohwer et al. 1989, Sealy & Bazin 1995, Peer & Sealy 2000).

Yellowish Flycatcher (*Empidonax flavescens*). There are no records of Bronzed Cowbird parasitism for this species.

Black Phoebe (*Sayornis nigricans*). Although not recorded as a host of the Bronzed Cowbird, there is a dubious record of parasitism by the Brown-headed Cowbird in California (Stoner 1938, Friedmann 1963).

Rufous-browed Peppershrike (*Cyclarhis gujanensis*). Though not recorded as a host of the Bronzed Cowbird, ejection of the artificial egg in the present experiment calls for additional nests to be tested to establish this species' response to parasitism. The few records of parasitism on this species by the Shiny Cowbird in Argentina (Friedmann 1929) offer little clarity, as a nest containing three host eggs plus two eggs of this parasite (Friedmann et al. 1977) suggests acceptance, at least by adults at this nest. As noted below in the account of the Clay-colored Thrush (*Turdus grayi*), artificial parasitism of >45 nests resulted in both responses to the artificial egg, with ejection recorded at ~18% of nests (Table 1). Eight nests were tested before the first ejection was recorded, which reveals the necessity of testing an appropriate number of nests of the species before assigning a response to cowbird parasitism. Observations of naturally parasitized nests suggest acceptance, but nests from which the cowbird's egg may have been ejected will be recorded as unparasitized, thus biasing the results (Peer et al. 2000, Klippenstine & Sealy 2008).

Cabanis's Wren (*Cantorchilus modestus*). The only report of parasitism for this species was of a fledgling Bronzed Cowbird fed in Honduras (Stone 1932, Friedmann 1963).

Clay-colored Thrush (*Turdus grayi*). Clay-colored Thrushes accepted the artificial egg at the single nest experimentally parasitized at La Selva, but ejected artificial eggs from eight (17.8%) of 45 nests at El Copey that were not depredated. To my knowledge, only two unsubstantiated records of parasitism on this species have been reported (Friedmann et al. 1977).

Rufous-collared Sparrow (*Zonotrichia capensis*). Acceptance assigned in this study extends experimental results and observations of parasitism reported in previous studies of this species. Rufous-collared Sparrows have been observed feeding cowbird fledglings in Costa Rica and Guatemala (Villeda 1979, Sealy et al. 1997), and by the late 1980s it had become a common host of the Bronzed Cowbird near the Universidad de Costa Rica (see Sealy et al. 1997). In Argentina and Brazil, high frequencies and high success of parasitism on this species suggest acceptance of the eggs (King 1973, Cavalcanti & Pimental 1988). Among 34 potential host species of Shiny Cowbird tested experimentally by Mason (1986), infrequent desertion was recorded in three species, including the Rufous-collared Sparrow. Of 18 artificially introduced cowbird eggs, none was ejected, but three experimental nests were deserted. Although unlike ejection, desertion remained unconfirmed because the response may not have been to the cowbird egg, but possibly to another stimulus or disturbance at the nest. Fraga (1978) reported 7 of 29 parasitized nests deserted, but assumed the response was only due to cowbird eggs.

Common Chlorospingus (*Chlorospingus flavopectus*). There are no records of Bronzed Cowbird parasitism for this species.

Black-striped Sparrow (*Arremonops conirostris*). Added to early records of parasitism on this species in Costa Rica (Cherrie 1892, Friedmann 1933), four additional records of parasitism were documented by Sealy et al. (1997).

White-naped Brushfinch (*Atlapetes albinucha)*. Six early records of parasitism from Costa Rica (Cherrie 1892, Alfaro 1904) suggest acceptance. To this total are added recent records of this species rearing Bronzed Cowbirds (Sealy et al. 1997). Echoing Cherrie's observations of >100 years ago, Stiles & Skutch (1989) considered this species and those in the genus *Arremonops* among the Bronzed Cowbird's most frequently parasitized hosts in central Costa Rica.

Flame-colored Tanager (*Piranga bidentata*). Acceptance is suggested by a multiply parasitized clutch recorded in Costa Rica (Sealy et al. 1997) and an observation of a fledgling fed by a male of this species in Mexico (Hall 1965). Hall (1965) did not confirm the cowbird's identity, but surmised the young was a Bronzed Cowbird because adults of this species were seen in the area.

Passerini's Tanager (*Rhamphocelus passerinii*). There are no records of parasitism on this species, but responses to the artificial egg at all six nests tested in this experiment accords with observations of acceptance of two Bronzed Cowbird eggs at 2 of 35 nests of Cherrie's Tanager (*R. costaricensis*) inspected near Sierpe, a village 13 km SW of Palmar Sur, Puntarenas Province, Costa Rica (Kiff 1973). Both cowbird eggs hatched in each nest, but all of the young were depredated. Originally classified as the same species –the Scarlet-rumped Tanager (*Rhamphocelus passerinii*)–, molecular genetic studies revealed two geographically distinct species: Passerini's Tanager, of the Gulf-Caribbean slope of Mexico and Central America, to western Panama and the northern Pacific Slope of Costa Rica, and Cherrie's Tanager of the southern Pacific Slope of Costa Rica and Panama (Hackett 1996).

Blue-gray Tanager (*Thraupis episcopus*). Not recorded as a host of the Bronzed Cowbird, but G.K. Cherrie recorded a nest parasitized by the Shiny Cowbird in Venezuela (Friedmann 1929).

Palm Tanager (*Thraupis palmarum*). There are no records of Bronzed Cowbird parasitism for this species, but there are at least two records of parasitism by the Shiny Cowbird in Brazil (Friedmann 1934, 1963).

Buff-throated Saltator (*Saltator maximus*). This species was first recorded as a host of the Bronzed Cowbird in Costa Rica

in 1986 (Sealy et al. 1997).

In general, and in spite of the small sample sizes of nests of most species tested, most species were recorded as acceptors, which is similar to the results of other studies of cowbird hosts (Rothstein 1975, Mason 1986), with the few cases of rejection accompanied by ejection of the parasitic egg. A departure from the usual all-or-none response by hosts –acceptance or rejection of all parasitic eggs– was shown in the Clay-colored Thrush, backed by tests of a large number of nests. Although artificial eggs were accepted at most nests, cowbird eggs were ejected from 17% of nests tested. Acceptance of different cowbird egg morphs by one of two other species of *Turdus* tested experimentally, the Creamy-bellied Thrush (*T. amaurochalinus*), was recorded in Argentina (Mason (1986). In contrast, and with large sample sizes, American Robins (*T. migratorius*) ejected Brown-headed Cowbird eggs at frequencies of nearly 100% (Rothstein 1975, Underwood & Sealy 2006). A mixture of acceptance and ejection by hosts is rare in temperate environments (Rothstein 1975), but whether it is more common in tropical environments awaits testing of more species.

Acceptance was assigned for each of 10 species, based on results from only one to three manipulated nests, but also for three species at which 6-10 nests were tested. Additional tests are required to determine whether acceptance or a mixed response is the prevalent response of the Tropical Kingbird and other tropical species of *Tyrannus* (also see Mason 1986). Tropical Kingbirds accepted all cowbird eggs in the present study, whereas the Fork-tailed Kingbird (*T. savanna*) was assigned ejection based on the ejection of all 7 eggs from nests tested in Argentina (Mason 1986), and a mixture of acceptance and ejection of artificial eggs was recorded in Brazil (Cavalcanti & Pimentel 1988). Cowbird eggs are usually ejected by temperate-nesting kingbirds at frequencies of nearly 100% (Peer & Sealy 2000). Sample sizes for most species are too small to permit comparison of responses of temperate and tropical species to cowbird parasitism.

Results of this experiment further substantiate the necessity of egg manipulation before responses of acceptance and rejection can be assigned. Observations of parasitized nests may suggest acceptance, but nests from which a cowbird egg has been ejected may be missed before the investigator next inspects the nest (Sealy & Bazin 1995). Timing of desertion may be pin-pointed following experimentation, but whether the response is to experimental parasitism or to another stimulus cannot always be confirmed without an appropriate control (Hill & Sealy 1994). Species observed feeding fledged cowbirds generally have been assumed to be the hosts –probably correctly in most cases–, but fledglings have been reported being fed by more than one species (Sealy & Lorenzana 1997). Further experiments should generate the much-needed quantitative data to establish the relative frequency of host choice throughout the range of the Bronzed Cowbird.

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