

INFREQUENT EJECTION OF ARTIFICIAL BRONZED COWBIRD (*MOLOTHRUS AENEUS*) EGGS BY THE CLAY-COLORED THRUSH (*TURDUS GRAYI*) IN COSTA RICA

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Resumen. – *Turdus grayi* rechaza con poca frecuencia huevos artificiales de *Molothrus aeneus* en Costa Rica. – *Turdus grayi* se ha reportado sólo en dos ocasiones como hospedero de *Molothrus aeneus*, aunque potencialmente podría estar disponible como tal. Hicimos pruebas de la respuesta de *Turdus grayi* que viven a elevaciones intermedias en Costa Rica a huevos artificiales de *Molothrus aeneus* que fueron colocados en sus nidos para determinar si el uso poco frecuente de esta especie como hospedero se debe al efecto del rechazo o si la rareza de parasitismo refleja la evasión por parte del parásito. *Turdus grayi* rechazó los huevos artificiales de *Molothrus aeneus* en 8 (17.8%) de 45 nidos y el parasitismo natural no fue registrado en ninguno de los nidos parasitados experimentalmente. La baja frecuencia de parasitismo reportada por *Molothrus aeneus* en *Turdus grayi* no se debe al rechazo de los huevos. Los pocos *Turdus* que rechazaron huevos se localizaron en áreas donde había más *Molothrus* y esta interacción podría influir la decisión de rechazar huevos. Estos resultados contrastan con el sistema *Turdus-Molothrus* de la zona templada, donde los primeros usualmente rechazan huevos. Se requieren experimentos de defensa de nidos, intercambio de huevos y pollos y manipulaciones de puestas en otras poblaciones para entender mejor este sistema de parásito-hospedero y porqué los *Molothrus* de los trópicos parecen evitar *Turdus* como sus hospederos.

Abstract. – We recorded the responses of Clay-colored Thrushes (*Turdus grayi*) at a middle elevation in Costa Rica to artificial Bronzed Cowbird (*Molothrus aeneus*) eggs placed into their nests to determine whether the infrequently observed use of this species as a host is an artifact of egg ejection, or whether the reported rarity of parasitism reflects non-use by the parasite. Clay-colored Thrushes ejected artificial Bronzed Cowbird eggs from 8 (17.8%) of 45 experimentally parasitized nests; natural parasitism was not recorded at any of these nests. The infrequency of reported parasitism by Bronzed Cowbirds on Clay-colored Thrushes is probably not an artifact of egg ejection. The few thrushes that ejected model eggs were in areas of higher observed cowbird density, thus interaction with cowbirds may influence the decision to eject. These results contrast with a temperate *Turdus-Molothrus* system, where cowbird eggs are usually ejected. Nest defense and cross-fostering experiments, and clutch manipulations in this and other populations, and in other species of *Turdus*, are required to better understand this tropical host-parasite system, and specifically why Bronzed Cowbirds seem not to parasitize Clay-colored Thrushes. Accepted 23 January 2012.

Key words: Bronzed Cowbird, Clay-colored Thrush, clutch manipulation, parasitism, Costa Rica, ejection, *Molothrus aeneus*, *Turdus grayi*.

INTRODUCTION

Instead of caring for their young, obligate avian brood parasites divert all parental care to the host species. They accomplish this by laying their eggs in nests of other species and evolving adaptations to circumvent host rejection (Johnsgard 1997, Rothstein & Robinson 1998, Davies 2000). Some brood parasites use only a few host species despite the availability of other potentially suitable species (Rothstein *et al.* 2002). Observed frequencies of natural parasitism may cloud our understanding of host-use by brood parasites because low frequencies reported on some species may reflect either rapid ejection of parasitic eggs or infrequent use of species as a host (Friedmann *et al.* 1977). Experimental parasitism is required to determine whether rapid ejection by hosts or avoidance by parasites is occurring in species infrequently reported as parasitized (Sealy & Bazin 1995).

Bronzed Cowbirds (*Molothrus aeneus*) are generalist obligate brood parasites whose eggs have been reported in nests of about 100 species, of which 44 are known to have raised them (Ellison & Lowther 2009). Knowledge of the Bronzed Cowbird's host-use, however, is incomplete because relatively few records of parasitism have been reported, particularly in the tropical portion of the cowbird's range (Sealy *et al.* 1997). Yet, despite laying in the nests of many species, Bronzed Cowbirds seem not to use nests of many potentially suitable host species (Sealy *et al.* 1997).

To our knowledge, only two unsubstantiated records of parasitism by Bronzed Cowbirds on the Clay-colored Thrush (*Turdus grayi*) have been reported (Friedmann *et al.* 1977) despite this thrush's potential suitability as a host: its nest is conspicuous, its breeding range overlaps with the cowbird's breeding range, and both species have similar diets (Rothstein 1975). These putative records from Chiapas were reported by Miguel Alva-

rez del Toro (Friedmann *et al.* 1977). Neither the years in which these observations were made nor the responses of the hosts were given. Therefore, we do not know whether the infrequent reports of parasitism on the Clay-colored Thrush reflect ejection of cowbird eggs before they can be recorded or whether cowbirds do not parasitize them in the first place. We recorded the responses of the Clay-colored Thrush in Costa Rica to experimental parasitism with artificial Bronzed Cowbird eggs.

METHODS

Study site. This study was conducted in and around the towns of El Copey de Dota (9°39'N, 83°55'W) and Santa Maria de Dota (9°39'N, 83°58'W), Costa Rica. El Copey and Santa Maria are approximately 25 km south of the city of Cartago on the Pacific slope of the Talamanca mountain range at c. 1850 m a.s.l. Both towns are situated along the Pirris River and its tributaries. Habitat varied between large apple orchards, cloud forest, cattle pastures, and the forested fringes of the above habitats, tributaries, and the more densely occupied town sites (Kappelle *et al.* 1992). In general, the low-lying and riparian areas tended to be used by humans, whereas higher elevation sites remained as cloud forests. Because we saw few cowbirds or thrushes in the cloud forest, we tended to avoid those habitats except where small fragments formed part of the human-altered mosaic. Nests were tested in El Copey de Dota from 22 March to 13 April 1999, 17 March to 9 April 2007, and 4 to 27 April 2008, corresponding with the end of the dry season. In 2008, five nests were tested in Santa Maria de Dota, Costa Rica from 7 to 19 April.

Study species. The Clay-colored Thrush is distributed from southern Texas to northern Colombia (Stiles & Skutch 1989, Brush 2000,

Clement 2000, del Hoyo *et al.* 2005). In Costa Rica, it is abundant in most habitats up to 2450 m a.s.l. and breeds from March to July, occasionally also in February and August (Stiles & Skutch 1989, Clement 2000, del Hoyo *et al.* 2005). The modal clutch size is three eggs (range 1–4 eggs, $N = 60$) and incubation requires 12 or 13 days (Dyrzc 1983). Asynchronous hatching of clutches suggests incubation typically begins with the laying of the penultimate egg (Dyrzc 1983). In this study, we defined the beginning of incubation as the day the penultimate egg was laid. To our knowledge, this species has been recorded parasitized by only the Bronzed Cowbird.

In the summer, Bronzed Cowbirds range from southeastern California, in the Little Colorado River Valley, southernmost Nevada, southwestern New Mexico, southeastern Arizona, southern Texas, southeastern Louisiana, and extreme southern Mississippi to northern Colombia (Attwater 1892, Moldenhauer 1974, Kostecke *et al.* 2004, Ellison & Lowther 2009). Bronzed Cowbirds are typically present at low elevations in the tropics but they have been recorded at altitudes of 1850 m a.s.l. (Johnsgard 1997, this study). There is one record of a Bronzed Cowbird egg in a Black-billed Nightingale-Thrush (*Catharus gracilirostris*) nest at 2400 m a.s.l. (Kiff 1973). In Costa Rica, where the Bronzed Cowbird lays eggs from March to July, 19 host species have been documented (Friedmann *et al.* 1977, Friedmann & Kiff 1985, Sealy *et al.* 1997). Laying lasts only 5–10 seconds (Peer & Sealy 1999a). Females often pierce a single egg in the nest when they lay their own to possibly reduce competition between host nestlings and their own offspring (Carter 1986, Peer & Sealy 1999b). Incubation was 10, 11, 11, and 12 days at four nests in southern Texas that were visited daily from the day the last egg was laid to the day it hatched (Carter 1986). Thrushes fledge at 10 ($N = 1$), 11 ($N = 7$), or 12 ($N = 6$) days (Carter 1986). In addition to the Clay-colored

Thrush and Black-billed Nightingale-Thrush, parasitism by the Bronzed Cowbird has been reported on several other species in the family Turdidae: Orange-billed Nightingale-Thrush (*C. aurantirostris*) (Thurber & Villeda 1980), Russet Nightingale-Thrush (*C. occidentalis*), and Rufous-backed Robin (*T. rufopalliatus*) (Friedmann & Kiff 1985).

Experimental parasitism. We inserted artificial Bronzed Cowbird eggs in Clay-colored Thrush nests that contained one or more host eggs during the laying or incubation stages. We inspected nests daily for five days to determine whether Clay-colored Thrushes accepted or rejected the artificial cowbird egg (either by ejection of the egg or by nest desertion). Artificial Bronzed Cowbird eggs were considered ejected if they went missing from active nests within 5 days and accepted if they remained undamaged in active nests for at least 5 days. Less than 1% of rejections occur after 5 days (Rothstein 1975, 1982; Lorenzana & Sealy 2001). Therefore, eggs accepted for 5 days are likely also to be accepted for the remainder of the nest attempt. Nests were considered depredated if all host and artificial eggs were gone or were damaged during the 5-day test period and deserted if eggs were cold and hosts were not seen near the nest during two successive daily inspections of the nest. At all but one nest where ejections were recorded, we inserted a second artificial egg into the nest to confirm the result.

We constructed artificial eggs of plaster-of-Paris to simulate the appearance of real Bronzed Cowbird eggs. Artificial eggs contained polystyrene foam cores to reduce their weight and were painted and polished to simulate the light bluish green color and smooth texture of Bronzed Cowbird eggs (Ellison & Lowther 2009). Clay-colored Thrush eggs are light blue with a high density of gray and reddish-brown maculations. A subsample of artificial eggs used in this experiment averaged

(mean \pm SD) 23.8 ± 0.5 mm (range 22.8–25.1 mm) by 18.3 ± 0.2 mm (range 17.6–18.8, $N = 58$) and weighed 4.8 ± 0.4 g (range 4–5.4 g, $N = 49$). The eggs of nominate *aeneus* measured 23.6 mm (range 21.37–25.19) by 18.4 mm (range 17.43–19.41, $N = 23$) (Ellison & Lowther 2009). The mean mass of real Bronzed Cowbird (*aeneus*) eggs is 3.91 g ($N = 78$) (Ellison & Lowther 2009).

Nest locations and cowbird sightings. We plotted the location of each thrush nest on a map in 2007 and 2008 and recorded the number of female and male cowbirds and their locations on 13 days in 2007 and 10 days in 2008 during nest-searching. Although we recorded cowbirds as they were encountered, they presumably reflected the locations where we searched for and found nests, and were biased towards habitats with greater visibility and detectability. Nonetheless, the habitat preference of cowbirds for open areas meant that detectability was likely quite high, potentially minimizing that bias. We assumed a female home range of 5–40 ha, as home range sizes of 5–20 ha have been reported for the smaller Brown-headed Cowbird (*M. ater*) (Darley 1982, 1983; Dufty 1982, Teather & Robertson 1985). We created a 10-ha circle around each female cowbird location, and for each day that a circle intersected a given nest, we counted one “cowbird-day”. Our assumption of a 10-ha home-range size did not bias our results, as cowbird-days at a given nest were highly correlated across a variety of home-range sizes (10 ha vs 5 ha: $R^2 = 0.82$; 10 ha vs 20 ha: $R^2 = 0.88$; 10 ha vs 40 ha: $R^2 = 0.79$).

RESULTS

We inserted artificial Bronzed Cowbird eggs into 51 Clay-colored Thrush nests: 8 in 1999, 19 in 2007, and 24 in 2008. Six (11.8%) of the 51 nests were depredated during testing. None of the nests tested was deserted. Arti-

cial eggs were accepted or ejected at 37 (82.2%) and 8 (17.8%) of 45 nests, respectively. Of these, two ejections and three acceptances were recorded in Santa Maria de Dota. There was no significant difference in ejection frequency between the laying stage (1 of 12 ejected) and incubation stage (6 of 32 ejected; Fisher exact test, two-tailed, $P = 0.6532$, $N = 44$). Modal clutch size of experimentally parasitized nests was three thrush eggs (range 1–3, $N = 47$), where clutch size was determined.

Ejection occurred between the time of insertion of an artificial egg and the next nest inspection, which occurred within a mean of 22 h 46 min (range 19 h 15 min–25 h 28 min) after parasitism at seven of eight nests. The other ejection occurred at a nest that was not checked again until 118 h 16 min after parasitism. We re-parasitized seven of the eight nests at which we recorded ejections to confirm the response. Second ejections, recorded as the time between insertion of the second artificial egg and the next time the nest was inspected, occurred within a mean of 20 h 17 min after parasitism (range 3 h 15 min–25 h 28 min) at six of seven nests. Ejection occurred at the other re-parasitized nest between 17 min and 54 h 28 min after parasitism. We did not record natural parasitism by Bronzed Cowbirds at any of the 51 experimental Clay-colored Thrush nests.

Bronzed Cowbirds were recorded several times in 2007 and almost every day in 2008 during the fieldwork at El Copey de Dota. We observed an average of 5.4 ± 1.8 (2007) and 3.2 ± 2.1 (2008) female cowbirds per day, and observed several courtship displays throughout the study periods. Cowbird-days were higher at nests where ejections occurred than at nests at which the cowbird eggs were accepted (2008: $t_{18} = 2.12$, $P = 0.048$; 2007 and 2008 combined: $t_{35} = 3.15$, $P = 0.003$). We observed only a single ejection in 2007, so no statistical comparison was made that year.

Cowbirds were most abundant on the cattle pastures along the main river above El Copey de Dota, where three out of seven thrushes (two out of five in 2008) ejected, and in the more densely populated regions along the river between El Copey de Dota and Santa María de Dota, where three out of six thrushes ejected (all in 2008). By contrast, we observed few cowbirds in the El Copey de Dota town site, or in the forested riparian strip along the tributary leading southeast of El Copey de Dota; we recorded only one ejection (in 2008) at these locations (out of 15 nests in 2007 and 9 nests in 2008). Cowbird-days were not higher for depredated nests than non-depredated nests (2007: $t_{21} = 0.32$, $P = 0.102$, 2008: $t_{17} = 0.51$, $P = 0.67$, combined: $t_{42} = 0.20$, $P = 0.131$).

DISCUSSION

Few Clay-colored Thrushes ejected artificial Bronzed Cowbird eggs but the ejections that occurred were consistently rapid and repeated, which suggests there is a mixture of acceptors and ejectors in this population (see Peer *et al.* 2002). The high frequency of acceptors suggests that the rarity of reports of parasitism on Clay-colored Thrushes by Bronzed Cowbirds is not solely an artifact of egg ejection. In addition, the scarcity of reports of parasitism by Bronzed Cowbirds on Clay-colored Thrushes likely is not due to a lack of Clay-colored Thrush nest monitoring because Morton (1971), Dyrce (1983), and we monitored 56, 83, and 51 Clay-colored Thrush nests, respectively, without recording natural parasitism. However, these nests were monitored in Panama and Costa Rica and the frequency of parasitism on Clay-colored Thrushes at other locations within their range is not known.

Our study adds the Clay-colored Thrush to the short list of host species that reject cowbird parasitism at an intermediate fre-

quency (see also Wiley 1982, Cruz *et al.* 1985, 1989; Post *et al.* 1990). Most species either accept or reject cowbird parasitism and the presence of accepters and rejecters within a population is rare (Rothstein 1975, 1990; Peer *et al.* 2002). The reason for the rarity of this result is that if ejection appears within a population it may be selected and reach fixation quickly (Rothstein 1975, 1990; Hosoi & Rothstein 2000). However, costs associated with ejection, such as mistakenly ejecting one's own egg, may offset the benefits when parasitism frequencies in a population are low (Davies *et al.* 1996, Brooke *et al.* 1998, Lorenzana & Sealy 2001, Rothstein 2001).

Other possibilities could account for the low ejection frequency in our study population. The parasitism pressure suffered by the Clay-colored Thrush population we tested may be low compared to other populations and thus ejection may not have been selected (Briskie *et al.* 1992, Thompson 2005, Røskft *et al.* 2006). Individuals that ejected Bronzed Cowbird eggs in the population we tested may have emigrated from other populations that experienced higher frequencies of parasitism, where ejection was selected (Underwood *et al.* 2004, Thompson 2005, Røskft *et al.* 2006, Peer *et al.* 2007). In addition, thrushes may need to interact with the adult parasite to reject a parasitic egg (Guigueno & Sealy 2011), as individuals that ejected in our population nested in areas where we saw cowbirds most often. Thus, many individuals may have accepted the artificial cowbird egg because they did not sufficiently interact with the parasite. Specifically, thrushes may aggressively defend their nests and ejection of the egg may be partially instigated by aggressive interactions prior to ejection (see Guigueno & Sealy 2011 for an example in a host that buries/deserts parasitized nests). Experiments of the type we performed should be conducted at other locations within the Clay-colored Thrush's range.

Ejectors remove real parasitic eggs from their nests by grasping the entire egg in their bill, usually without damaging it, or by puncturing them with their bill and carrying them on their bill (puncture-ejection) (Sealy 1996, Underwood & Sealy 2006a, Honza *et al.* 2007, Rasmussen *et al.* 2009). The use of a hard material for making the artificial eggs may have prevented some Clay-colored Thrushes, if they were puncture-ejectors, from ejecting them, resulting in an underestimation of the true frequency of egg rejection in the population. However, the lack of peck marks on recovered artificial eggs suggests that none of the Clay-colored Thrushes tested attempted to puncture any of the artificial eggs.

The exclusion of the Clay-colored Thrush as a host species by the Bronzed Cowbird is puzzling because they reject parasitic eggs infrequently, are common, and have overlapping breeding seasons (Stiles & Skutch 1989). However, Bronzed Cowbirds may not parasitize Clay-colored Thrushes for other reasons. First, the high variability in the time between nest building and egg laying (i.e., 2–10 days, mean = 5.3 days, N = 18; Dyrz 1983), similarity of incubation periods (Dyrz 1983, Carter 1986) and the short egg-laying period (3 days) may make it difficult for cowbirds to synchronize their lay dates so that their eggs hatch before or at the same time as thrush eggs (De Marsico & Rebores 2008). Carter (1986) found that all Bronzed Cowbirds that hatched 48 hours after the host nestlings in 10 nests did not survive. On the other hand, the cowbirds may fledge if they hatch at the same time or sooner than larger hosts (see Peer & Bollinger 1997, Peer & Sealy 2004). Second, thrushes may use aggressive nest defense behavior (Sealy *et al.* 1998, Guigueno & Sealy 2011) or have patterns in nest attentiveness (Arcese & Smith 1988, Uyehara & Narins 1995, Neudorf & Sealy 1994, Fiorini *et al.* 2009) that reduce susceptibility to cowbird parasitism. Third, parasite nestlings may have

low success in thrush nests (for examples in other hosts see Langmore *et al.* 2003, Schuetz 2005, Astié & Rebores 2009, Remes 2010, Sato *et al.* 2010). Although the mechanisms are quite different, *Turdus* spp. are seldom parasitized by cuckoos because they are unsuitable hosts during the nestling period (Grim *et al.* 2011).

We provide some of the first experimental documentation of host-brood parasite interactions between the Bronzed Cowbird and Clay-colored Thrush in a tropical environment. With our substantial sample size across three years, we showed an intermediate level of ejection in this host of a brood parasite. By contrast, in the American Robin (*T. migratorius*)-Brown-headed Cowbird interaction at temperate latitudes, American Robins usually eject at frequencies of nearly 100% (Rothstein 1982, Underwood & Sealy 2006b). In general, intermediate ejection is rare in temperate environments but may be more common in tropical environments based on the few species tested to date (Wiley 1982, Cruz *et al.* 1985, 1989; Post *et al.* 1990). Cross-fostering experiments, additional study of host-parasite behavioral interactions, and testing of more potential hosts are needed to determine whether different life-history strategies in tropical bird species, relative to temperate birds, truly lead to different anti-parasite strategies for tropical hosts.

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