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PARASITISM BY SHINY COWBIRDS OF RUFOUS-BELLIED THRUSHES[1]

GABRIELA LICHTENSTEIN[2]
Department of Zoology, University of Cambridge, Downing Street, CB2 3EJ Cambridge, U.K., e-mail: gll1000@cus.cam.ac.uk

Abstract. I studied the interaction between a brood parasite, the Shiny Cowbird (*Molothrus bonariensis*), and a large host, the Rufous-bellied Thrush (*Turdus rufiventris*), in the Pampas Region of Argentina. Shiny Cowbird eggs were observed in 34 out of 70 (48.6%) thrush nests throughout the host's breeding season. The main damage inflicted by Shiny Cowbirds was the puncture of host eggs, which occurred in 55.9% of the parasitized nests and significantly reduced the host clutch size. Because of the host's short incubation period, cowbird eggs did not hatch more than one day before the host young. This small advantage of earlier hatching was not enough to outweigh the large size difference between the parasitic chicks and the host young. In 68.7% of experimentally-created broods containing one host and one cowbird chick, the cowbird chicks died of starvation. I conclude that the Rufous-bellied Thrush is a particularly poor host for Shiny Cowbirds because of its large size and short incubation period. The high rate of parasitism, even of such a poor host, indicates little selectivity by Shiny Cowbird females.

Key words: brood parasitism, host selection, Molothrus bonariensis, *parasitic chicks, Rufous-bellied Thrush, Shiny Cowbird,* Turdus rufiventris.

INTRODUCTION

Although it has been suggested that Shiny Cowbirds prefer to parasitize hosts larger than themselves (Mason 1980), studies of the interaction of Shiny Cowbird chicks with larger hosts show that on most occasions Shiny Cowbird chicks starved in nests of larger species. Gochfeld (1979) found that 96% of Meadowlark *Sturnella loyca* nests were parasitized by Shiny Cowbirds, but none of them produced a cowbird fledgling. A study by Fraga (1978) showed that 37% of Shiny Cowbirds starved in Chalk-browed Mockingbird *Mimus saturninus* nests. The only case in which the Shiny Cowbirds did well at nests of larger hosts was when parasitizing Brown-and-Yellow Marshbirds (Mermoz and Reboreda 1994). However, this result could be due to the combined effect of helpers at the nest and the shorter incubation period of the cowbird eggs.

This paper has two aims: the first is to provide natural history information on the interaction between the Shiny Cowbird and a common large host with a short incubation period, the Rufous-bellied Thrush *Turdus rufiventris,* and the second is to discuss whether these findings support Mason's (1980) hypothesis that Shiny Cowbirds prefer to parasitize large hosts rather than small ones.

METHODS

STUDY SPECIES

The Rufous-bellied Thrush is a medium sized sexually monomorphic thrush that weighs around 70–80 g. It is a typical member of its genus and one of eight *Turdus* species that breed in Argentina. The Rufous-bellied Thrush breeds throughout northern Argentina (from the South of Cordoba and Buenos Aires), Uruguay, Paraguay, eastern Bolivia, and eastern Brazil. It is common in open woodland, forest borders, clearings, and gardens (Ridgely and Tudor 1989). The breeding season in the area of Buenos Aires starts in late August/September, and extends until the end of December. The open nest is made of twigs and mud, and the clutch of bluish eggs with spots varies from 2–6 with a mode of 3 eggs per nest. Incubation starts after laying the second egg, and lasts for 13 days. Both parents feed the nestlings, which fledge after about 13 or 14 days and which receive parental care for a further period of about 14 days. Pairs typically raise two broods per season. The adult diet consists mostly of invertebrates (especially earthworms) and fruits. Adults feed the young with earthworms, insects, and berries. Rufous-bellied Thrushes are parasitized by

[1]Received 30 June 1997. Accepted 17 July 1998.
[2]Current address: International Institute for Environment and Development-AL, Gral Paz 1180, (1429) Buenos Aires, Argentina, e-mail: gaby@interlink.com.ar

TABLE 1. Incidence and intensity of parasitism of Rufous-bellied Thrushes by Shiny Cowbirds during the season.

Month	Total nests	Nests with cowbird egg	Parasitism rate[a]	No. of cowbird eggs	Cowbird eggs per parasitized nest[b] (mean ± SE)
October	26	12	46.1%	16	1.33 ± 0.26
November	33	14	42.4%	18	1.29 ± 0.16
December	11	8	72.7%	19	2.37 ± 0.65
Total	70	34	48.6%	53	1.56 ± 0.19

[a] χ^2 on original numbers = 3.1, $P = 0.21$.
[b] χ^2 comparing nests with one versus two or more eggs = 3.0, $P = 0.21$.

Shiny Cowbirds (Friedmann et al. 1977), but the interactions between them have never been studied in detail.

STUDY SITE AND NEST VISITS

The study was conducted at parks and gardens in the locality of Del Viso (34°29′S, 58°35′W), in the Province of Buenos Aires, Argentina, from October 1994 to January 1995. Thrush nests were located usually between 1.6 and 4.0 m above the ground in the forks of trees, in vines, dense bushes, ornamental vegetation, or in fruit trees. I monitored daily the progress of a total of 70 nests, recording the number of parasitic and host eggs present and the order of laying and hatching. Nests were considered parasitized if they contained cowbird eggs or nestlings at any stage. I did not consider nests which had missing host eggs, but no cowbird eggs, to have been parasitized.

Eggs were examined for punctures and measured with vernier calipers to the nearest 0.1 mm. The incubation period was measured from the day the penultimate egg was laid until each egg hatched. Once eggs had hatched, I manipulated nest contents to create broods containing one thrush and one Shiny Cowbird chick of the same age (± 1 day) in order to standardize nest contents. The remaining host or Shiny Cowbird chicks were cross-fostered to nearby nests containing chicks of approximately the same age. Chicks were weighed daily between 06:00 and 08:00 with a 50 g Pesola spring balance, until the age of 12 days. Tibia, gape length, and gape width were measured to the nearest 0.1 mm with vernier calipers. I used Ricklefs' (1967) method to estimate the growth constant (K) and compare the growth rate of the cowbird and the thrush chicks.

Information about the type of food delivered to the chicks was extracted from video taping of nine nests when the chicks were 7 days old. Ten hours of video recordings were analyzed per nest.

I used nonparametric analysis because of the small sample sizes (Siegel and Castellan 1988). All tests were two-tailed, and results are reported as significant if $P \leq 0.05$. Values reported are means ± SE unless otherwise specified.

RESULTS

INCIDENCE AND INTENSITY OF PARASITISM

Shiny Cowbird eggs were observed in 34 out of 70 (48.6%) Rufous-bellied Thrush nests found during the egg stage. The size of host clutches was reduced due to egg puncture in a further 10 nests, but no parasitic eggs were found. As nests with missing or punctured thrush eggs were not considered parasitized unless they had a cowbird egg, the observed incidence of parasitism might be an underestimate because cowbird eggs may have been rejected by the hosts before I had the chance to record them (see below). The incidence of parasitism reached a peak in December (Table 1), coinciding with a decrease in the number of potential host nests available. Multiple parasitism (more than one cowbird egg per nest) occurred in 24.5% of the parasitized nests (Fig. 1) and also reached a peak in December. However, neither of these trends was statistically significant (Table 1).

EGG MORPHS

Cowbird eggs measured 22.70 ± 0.26 mm in length and 18.00 ± 0.09 mm in width ($n = 34$). Rufous-bellied Thrush eggs were larger, measuring 27.10 ± 0.24 mm in length and 20.80 ± 0.01 mm in width ($n = 20$). Fifty-two out of 53 (98.1%) cowbird eggs found in this study were spotted, whereas only one was of the immaculate morph.

EGG PUNCTURE

Shiny Cowbirds often puncture host eggs (Fraga 1985). Although there was no difference in the

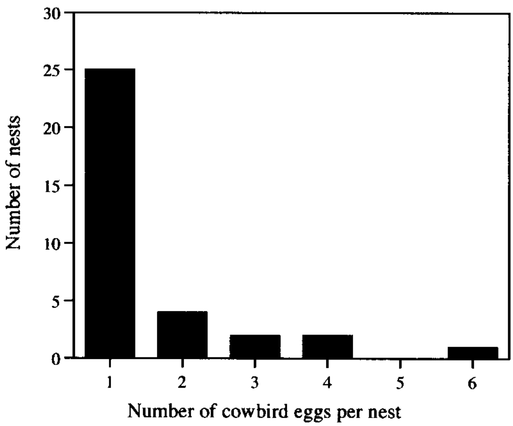

FIGURE 1. Frequency distribution of number of observed Shiny Cowbird eggs per nest of Rufous-bellied Thrush.

number of eggs laid by thrushes in parasitized and nonparasitized nests (Table 2), the number of host eggs present at the time of hatching was significantly smaller in parasitized nests. This was due to egg puncture by the Shiny Cowbirds.

From the 34 parasitized nests, 19 (55.9%) lost at least one host egg due to puncture. Host eggs disappeared or were punctured in 10 (27.8%) of the nonparasitized nests ($\chi^2_1 = 5.69$, $P = 0.02$). In five parasitized and one nonparasitized nest, egg puncture was followed by desertion. Two cowbird eggs were found punctured in multiply parasitized nests. Shiny Cowbird eggs disappeared in four of the parasitized nests. These eggs may have been rejected outright, or else have been punctured by female cowbirds before being ejected by the hosts.

EGG LAYING

The incubation period was 13 days for the thrushes (range 12–13 days, $n = 16$ nests) and 12 days for the cowbirds (range 11–13 days, $n = 12$ nests). In clutches of three eggs, female thrushes started incubation after laying the second egg, which resulted in asynchronous hatching. The first two thrush chicks hatched the first day (usually 0.5 day apart), whereas the third chick hatched the following day. Most of the unhatched eggs were the eggs that were laid last.

Twenty-seven percent (7 of 26) of the cowbird eggs present at the end of the incubation period did not hatch. Three of these had developed embryos indicating that they were laid too late in the nesting cycle of the thrush, whereas the rest showed no sign of development. Of the hatched cowbird eggs with known histories, 89.5% of the chicks were born in the 3-day interval between 1 day before and 1 day after the date on which the first thrush chicks hatched (Fig. 2). Taking into account that the incubation period of the cowbird is only 1 day shorter than that of the thrush chicks, and that thrushes start incubation after laying the second egg, cowbird females have only 2 days to lay eggs that will hatch before or on the same day as the host young.

NEST SUCCESS

Five parasitized and one nonparasitized nest were deserted following egg puncture (Fisher exact test $P = 0.1$). Fourteen out of 35 (40%) nonparasitized and 10 out of 29 (34.5%) parasitized nests suffered from predation ($\chi^2_1 = 0.2$, $P = 0.65$). Nests were considered depredated if the entire clutch or brood disappeared. Likely mammalian predators include white-eared possums *Didelphis albiventris* and domestic cats. Chimangos *Milvago chimango* were the most likely avian predators. There was no difference in the predation rate at the egg stage of parasitized (6 out of 29) and unparasitized nests (9 out

TABLE 2. Results of Mann-Whitney *U*-tests comparing the number of host eggs present per parasitized and nonparasitized nest. The decrease in the number of eggs present at the end of the incubation period was due to egg puncture by female cowbirds.[a]

	Nonparasitized ($n = 36$)	Parasitized ($n = 34$)	z	P
Mean No. of host eggs laid	3.34 ± 0.12	3.14 ± 0.07	−1.35	0.18
Mean No. of host eggs present late in the incubation period	3.27 ± 0.16	2.31 ± 0.17	−4.52	<0.001

[a] There was no difference between the number of host eggs laid and the number of host eggs present late in the incubation period in nonparasitized nests (Wilcoxon sign ranks test, $z = -1.3$, $P = 0.18$). In parasitized nests the difference was significant ($z = -4.3$, $P < 0.001$).

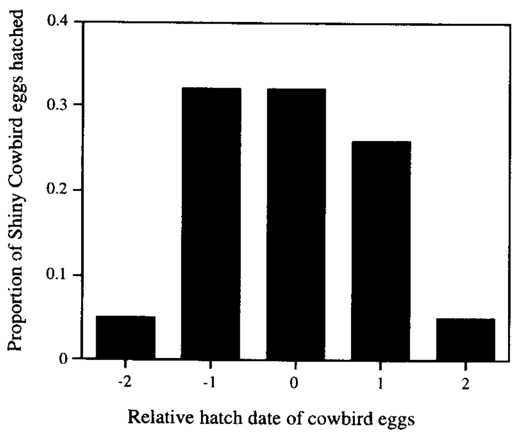

FIGURE 2. Relative date of hatching of Shiny Cowbird eggs ($n = 19$) in relation to the date of hatching of the first thrush egg in each nest. A relative hatch date of zero indicates that the cowbird and first thrush egg hatched the same day, positive values indicate that the cowbird egg hatched after the thrush egg, and negative values indicate that the cowbird egg hatched before the first thrush egg.

of 35, $\chi^2_1 = 0.2$, $P = 0.64$). Likewise, there was no difference at the nestling stage (4 out of 23 parasitized nests depredated, and 5 out of 26 unparasitized nests, Fisher exact test, $P > 0.1$). Therefore, the presence of a cowbird egg or chick did not seem to affect predation rates.

Shiny cowbird chicks starved in 11 out of 16 nests containing one thrush and one cowbird chick, whereas all 16 of the Rufous-bellied Thrush chicks at those nests fledged successfully ($\chi^2_1 = 16.8$, $P < 0.001$). Mortality occurred either when the chicks were 4–5 days old ($n = 7$), or late in the nesting period ($n = 4$). Because in a natural situation, Shiny Cowbird chicks are accompanied by one to three host young (not just one as here, due to my experimental manipulation), the frequency of brood reduction is probably an underestimate of its natural occurrence. Hatching before the host chicks did not decrease the chances of the Shiny Cowbird chick starving (6 out of 9 chicks that hatched before the thrush chick starved vs. 5 out of 7 that hatched the same day or one day after, Fisher exact test, $P > 0.1$).

NESTLING GROWTH AND APPEARANCE

From hatching, Shiny Cowbird chicks look very different from the Rufous-bellied Thrush nestlings. Nestling growth was monitored in 12 nests, each containing one Rufous-bellied Thrush and one Shiny Cowbird chick of the same age (± 1 day) (Fig. 3). Rufous-bellied Thrush nestlings hatch with a significantly wider (Mann-Whitney *U*-test, $z = -3.74$, $P = 0.001$) and longer ($z = -3.04$, $P < 0.01$) gape with a bright yellow mouth lining and yellow flanges, whereas the mouth lining of the gape of the Shiny Cowbirds is bright red, and the rictal flanges are white. The difference in gape size remains throughout the nestling period (Mann-Whitney *U*-test for data on the 10th day, $z = -3.43$, $P < 0.001$ for gape width, and $z = -2.86$, $P < 0.01$ for gape length). Figure 3b shows the increase in gape area through time for both species. The tibiae of Rufous-bellied Thrush chicks are significantly longer than those of the Shiny Cowbird chicks ($z = -3.45$, $P < 0.001$ at age 0, and $z = -3.42$, $P < 0.001$ at the age of 10 days, Fig. 3a).

Thrush chicks weighed significantly more than cowbird chicks at hatching (6.2 ± 0.4 g vs. 3.9 ± 0.3 g, Mann-Whitney *U*-test, $z = -3.55$, $P < 0.001$, Fig. 3c). The weight difference increased with age leading to an asymptotic weight for the thrush chicks which was 69.0% larger than the asymptotic weight of the Shiny Cowbird chicks (asymptotic weight A = 36 g for the Shiny Cowbirds and 61 g for the Rufous-bellied Thrush chicks, Mann-Whitney *U*-test, $z = -3.45$, $P < 0.001$). The growth rate of the thrushes was not significantly greater than that of the Shiny Cowbirds (K = 0.59 ± 0.04 and K = 0.53 ± 0.04, respectively; $z = -1.63$, $P = 0.10$).

NESTLING DIET

During the late nestling period, nestlings were fed mainly animal protein. Food loads were identified from the video recordings as earthworms, arthropods, or fruit. Earthworms (Oligochaeta) constituted 50.0 ± 0.9% of the food items brought to the nest ($n = 9$ nests), whereas arthropods represented 38.1% of the loads (27.2 ± 0.7% were Lepidoptera larvae and 10.9 ± 0.5% were Lepidoptera and Orthoptera). Fruit (berries) represented 7.3 ± 0.4% of the loads. I was not able to identify the remaining 4.6% of the food brought to the nest.

DISCUSSION

Rufous-bellied Thrushes are poor hosts for the Shiny Cowbirds. The combined effect of a much larger body size of the host young and a rela-

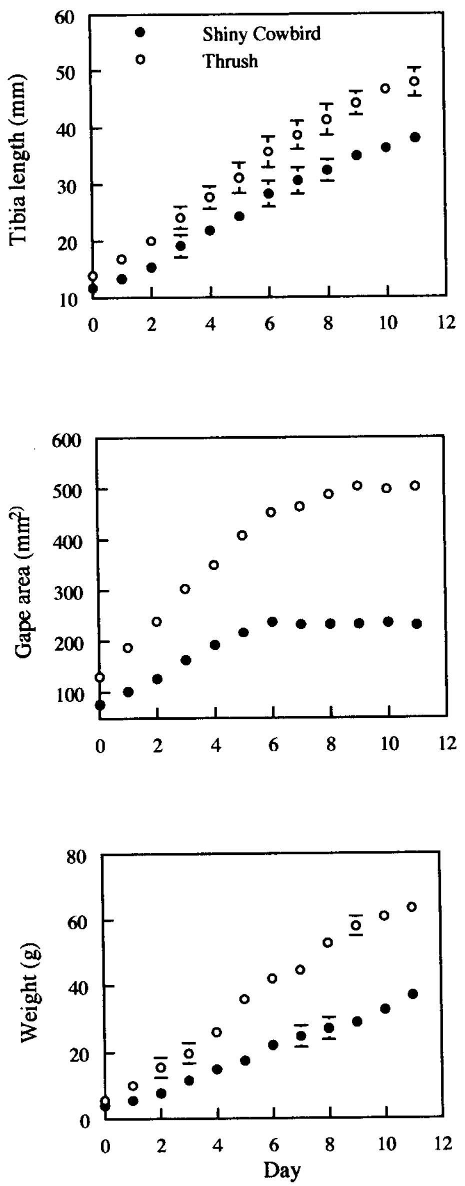

FIGURE 3. Comparison of nestling growth. The figure shows mean gape area and mean ± SD of tibia length and weight for Shiny Cowbirds and thrushes. Gape area is the product of gape length and gape width. Twelve thrushes were measured from day 0 to day 11. The number of cowbirds measured per day is: 7, 12, 12, 11, 9, 6, 7, 8, 8, 6, 6, 4. Data comes from 12 nests containing one thrush and one cowbird chick of the same age ± 1 day.

tively short incubation period resulted in Shiny Cowbird chicks starving in 68.7% of the parasitized nests. The high rate of parasitism, even of such a poor host, indicates little selectivity by Shiny Cowbird females or low densities of alternative hosts (Barber and Martin 1997).

Whereas Brown-headed Cowbirds manipulate host clutches by egg removal (Wood and Bollinger 1997), Shiny Cowbirds do so principally by puncturing their host's eggs. The main damage inflicted by Shiny Cowbirds in this study was the destruction of host eggs. Egg puncture was reported as the main damage caused by Shiny Cowbirds in nests of other large hosts such as Brown-and-Yellow Marshbirds (Mermoz and Reboreda 1994), and Chalk-browed Mockingbirds (Fraga 1982). In nests of smaller hosts, however, competition between cowbird and host chicks also strongly decreases the reproductive success of the host (Fraga 1978, Marvil and Cruz 1989). Egg removal and egg laying are not necessarily temporally coincident in cowbirds (Sealy 1992). Hence nests with punctured eggs but without parasitic eggs could have been due to females puncturing eggs and not being able to return later to lay their eggs, or to females laying eggs of the white morph that were rejected by the hosts.

The low frequency of eggs of the white morph in thrush nests and their presence in nests of other passerines breeding in the same area is indirect evidence for the hypothesis that Rufous-bellied Thrushes reject cowbird eggs of the immaculate morph. Rejection of the white morph by thrushes has been reported (Mason 1980), but experiments are needed to test this hypothesis. Other large hosts that lay spotted eggs, such as Brown-and-Yellow Marshbirds (Mermoz and Reboreda 1994) and Chalk-browed Mockingbirds (Fraga 1982), also reject eggs of the white morph.

WHY DO SHINY COWBIRD CHICKS DO SO BADLY IN RUFOUS-BELLIED THRUSH NESTS?

Diet incompatibility. An important factor which sometimes contributes to nestling starvation in cowbirds is dietary incompatibility with the host. Brown-headed Cowbirds fail to fledge in nests of hosts that feed their nestlings with seeds (House Finch, *Carpodacus mexicanus,* Kozlovic et al. 1996), fruit (Cedar Waxwing, *Bombycilla cedrorum,* Rothstein 1976), or other plant material (House Sparrow, *Passer domesticus,* Eastzer et al. 1980). Similar results were found for Shiny Cowbirds parasitizing Saffron Finches *Sicalis flaveola* (Mason 1980). However, the diet provided in Rufous-bellied Thrush nests consisted at least of 88% animal protein, which precludes dietary incompatibility as an explanation for the starvation of cowbird nestlings.

Large size difference with the host young. Rufous-bellied Thrush chicks weigh significantly more than the Shiny Cowbird chicks from hatching. There was no evidence that hatching before the host young could prevent cowbird chicks from starving. As a result of the short incubation period of the thrush, Shiny Cowbird chicks could not hatch more than 1 day before the host young; thus there was insufficient time for cowbird nestlings to attain body masses to negate the size difference and faster growth of host chicks. The result of this study is similar to that of previous studies on the interaction of Shiny Cowbird chicks and large hosts, showing that cowbird chicks are generally outcompeted by host young of a similar incubation period (Chalk-browed Mockingbirds, 13 days, pers. observ.). Having a shorter incubation period overcomes the size disadvantage of Shiny Cowbird chicks parasitizing greater Antillean Grackles *Quiscalus niger* (14 days, Wiley 1986). The longer incubation period of the Brown-and-Yellow Marshbird eggs (14–15 days, Mermoz and Reboreda 1994) might be an important factor in determining the success of Shiny Cowbird parasitizing this host.

Different appearance. The difference in appearance between the Shiny Cowbird and host nestlings also might have contributed to the poor success of the cowbird chicks. When parents arrive at the nest with food, they are faced with the open gapes of nestlings. Rufous-bellied Thrush adults might have an innate preference for yellow and wide gapes, in which case the big yellow gapes of thrush chicks could be a stronger stimulus for feeding than the much smaller red gape of the cowbirds. The combined effect of having a much smaller gape with a different color of rictal flanges and mouth lining might put cowbird chicks at a disadvantage for eliciting feedings. A difference in appearance might explain why Brown-headed Cowbird chicks (gapes with red lining and white rictal flanges) are outcompeted by the slightly larger Northern Cardinal (Scott and Lemon 1996; orange-red lining and white rictal flanges, Eckerle, pers. comm.), but do well at nests of larger hosts with a similar gape color, e.g., Yellow-headed Blackbird *Xanthocephalus xanthocephalus* (Ortega 1991). The idea that parents might discriminate on the basis of gape color is not new. In 1978, Rothstein hypothesized that the variation in the color of the rictal flanges of the cowbirds was influenced by the preferential feeding of those chicks whose gape is most similar to that of their own young. This might explain why, when parasitizing larger hosts, Shiny Cowbirds are more successful at parasitizing species with similar looking chicks. Icterids, which all have red gapes (Ficken 1965) are among the most common hosts of the Shiny Cowbird in South America (Friedmann et al. 1977), Trinidad and Tobago (Manolis 1982), and Puerto Rico (Wiley 1988). The more specialist species of parasitic cowbirds also parasitize Icterids (reviewed in Lichtenstein 1997).

In summary, the low success of the Shiny Cowbird chicks was probably due to their smaller size and/or having a different appearance. A study comparing the feeding success of parasitic cowbird chicks and similar sized thrush chicks showed that Shiny Cowbird chicks were fed only if the host chicks were not begging, suggesting that parental choice plays an important role in determining who gets fed in parasitized nests of Rufous-Bellied Thrushes (unpubl. data).

DO COWBIRDS PREFER TO PARASITIZE LARGE HOSTS OVER SMALLER ONES?

Mason (1980) suggested that Shiny Cowbirds prefer to parasitize large hosts over smaller hosts. Considering the low reproductive success of the Shiny Cowbird chicks in nests of large hosts, this preference seems maladaptive. I believe that Mason's conclusion was due to the fact that he included species with very small sample sizes in his analysis. In any case, host preference can not be determined unless the whole community of potential hosts is sampled. In just such a study of multiple coexisting host species, Barber and Martin (1997) showed that parasitism rates on Black-capped Vireos (*Vireo atricapillus*) were positively correlated with cumulative coexisting host density in general, and with Northern Cardinal (*Cardinalis cardinalis*) density in particular. This study shows the negative effect of coexisting species on the parasitism rate of a focal species and the importance of taking into account the entire host community.

If large hosts were preferred in the past, one would expect to find large hosts preferred in new areas of colonization of the Shiny Cowbirds. The invasion of the Caribbean by the Shiny Cowbird provides a natural test of this hypothesis. There is no evidence for Shiny Cowbirds preferring large hosts in newly colonized areas, such as Puerto Rico (Perez-Rivera 1986, Wiley 1988), or Santa Lucia (Post et al. 1990).

Additional evidence against a preference for large hosts comes from studies of parasitism of Shiny Cowbirds in other areas. In a previous study, the Rufous-collared Sparrow was reported to be the most frequent host in Argentina (King 1973), Uruguay and Brazil (Friedmann et al. 1977, Cavalcanti and Pimentel 1988), whereas the Diuca Finch *Diuca diuca* is the most frequent host in Chile (Johnson 1967), and the House Wren *Troglodytes aedon* in the Cauca Valley in Colombia (Kattan 1993). All of these hosts are smaller than the Shiny Cowbird.

In summary, I believe that with the evidence available we are not in a position to conclude that Shiny Cowbirds show an active preference to parasitize large hosts over small ones.

I agree with Mason that species larger than the cowbird are probably better hosts than smaller species in terms of bringing more food to the nest, having more structurally stable nests, providing better defense against nest predators, and having less concealed nests (i.e., which are easier to find for the parasite). However, this must be offset against the greater competition from large host young. The "ideal" hosts for the Shiny Cowbird might be similarly sized or slightly larger colonial Icterids with a relatively longer incubation period. Icterids not only inhabit similar areas as those of the Shiny Cowbirds, but they also have more similar looking eggs and chicks than members of nonrelated families. The disadvantage of the Icterids is that they usually are aggressive in defending their nests (Cruz et al. 1990).

WHY DO SHINY COWBIRDS SHOW A HIGH PARASITISM RATE ON POOR HOSTS?

The high parasitism rate of poor hosts (Gochfeld 1979) gives support to the argument of a generalist "shotgun" (Rothstein 1990, Kattan 1997) strategy. Instead of spending energy on searching for nests of the best species to parasitize, cowbirds seem to be following an opportunistic strategy in which factors such as host aggressiveness, attentiveness (Mason 1980), and availability of nests to parasitize seem to be important. The opportunistic strategy of the cowbirds contrasts with the specialist strategy of the European Cuckoo *Cuculus canorus* (Wyllie 1981). Cuckoos have a comparatively lower fecundity than cowbirds, and probably allocate more energy to selecting host nests and laying at a certain time. High fecundity and cheap egg production (Kattan 1995) might enable female cowbirds to pursue an opportunistic strategy, laying eggs in nests of poor hosts in the absence of higher quality hosts to parasitize. However, a generalist strategy is sometimes costly for cowbirds, as is shown by the high parasitism rate of such a poor host as the Rufous-bellied Thrush.

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