# REPRODUCTIVE INTERACTIONS OF THE SHINY COWBIRD AND THE YELLOW-SHOULDERED BLACKBIRD

WILLIAM POST
AND
JAMES W. WILEY

The Shiny Cowbird (*Molothrus bonariensis*) is a widespread brood parasite occurring from Patagonia to Hispaniola. The species is extending its range in South America (Johnson 1967) and in the Caribbean (Bond 1973). The race *M.b. minimus*, aided by man-made introductions (Post and Wiley 1977), has been expanding its range NW through the Caribbean since about 1860, when it was recorded in Vieques Island (Newton 1860). The Shiny Cowbird was first seen in Puerto Rico in 1955 (Grayce 1957), although it may have arrived before then (Post and Wiley 1977). In lowland Puerto Rico, where we conducted most of our work, we found the Yellow-shouldered Blackbird (*Agelaius xanthomus*) to be the main host of the cowbird. Seventy-six percent of 84 Yellow-shouldered Blackbird nests contained cowbird eggs, and brood parasitism reduced the reproductive output of the blackbird. *A. xanthomus*, endemic to Puerto Rico and Mona Island, has been declining since the 1940's, probably coincidental with the arrival of the Shiny Cowbird in Puerto Rico (Post and Wiley 1976, 1977).

A number of workers have described the general biology of the Shiny Cowbird (Hudson 1920, Friedmann 1929, 1963, Sick 1958, Hoy and Ottow 1964). Sick and Ottow (1958) and King (1973) made quantitative studies of the Shiny Cowbird's relationship with one of its main South American hosts, the Rufous-collared Sparrow (*Zonotrichia capensis*). However, there have been few other quantitative investigations of Shiny Cowbird reproduction, and no information is available concerning the relationships of this species with new hosts. In comparison with what is known about established brood parasite-host systems, such information elucidates the evolution of brood parasitism and host defenses against it.

## METHODS

We conducted detailed studies at two sites, one in SW Puerto Rico near La Parguera and the other in E Puerto Rico near Ceiba. The La Parguera study site (17°58′N) is within and on the edge of the Boquerón Commonwealth Forest, along the Caribbean coast. The study area extended 7 km SW from La Parguera, to 1 km past El Guayacán Island. At La Parguera Yellow-shouldered Blackbird nesting areas were in the coastal mangrove zone, in dry pastures with deciduous trees located along the mangroves, and on offshore mangrove cays. The climate around La Parguera is arid tropical, with a mean annual rainfall of 56 cm (12-year average recorded at La Cueva Island, 1962–1973). The Ceiba study site (18°15′N) is about 150 km ENE of La Parguera. The Ceiba study was conducted within the mangrove zone, also near the Caribbean coast on Roosevelt Roads Naval Station, 3 km SE of Ceiba. The climate at Ceiba is humid tropical, with a mean annual rainfall of about 148 cm.

At La Parguera the study was conducted from December 1972 to September 1975; at Ceiba from February to August 1975 and from May to August 1976. During the *A. xanthomus* breeding season (May–September) we visited each study area at least five times per week. We found 84 Yellow-shouldered Blackbird nests and 110 nests of other passerines. Blackbird nests were either given numbered tags or were located on field maps. We marked newly hatched birds by toe-clipping, and older nestlings with bands. Young were weighed between 09:00 and 11:00. We watched nests from portable blinds placed about 5 m away. Adult blackbirds and cowbirds were captured in mist nets placed around monkey feeding stations at the Caribbean Primate Research Center on La Cueva and El Guayacán Islands. We also trapped birds with Potter traps or with drop traps placed on feeding shelves baited with sugar or rice. All birds were marked with U.S. Fish and Wildlife Service bands and with color bands. During December 1972–May 1974 we color-banded 306 Yellow-shouldered Blackbirds. To collect data on their survival, we made surveys for these blackbirds at seven monkey and cattle feeding stations in SW Puerto Rico until February 1976. Roost counts of blackbirds were conducted throughout the year. Since all coastal roosts were on small offshore islands, it was easy for several observers stationed in a boat to cover major flight lines to the roosts.

## RESULTS AND DISCUSSION

### DISTRIBUTION OF SHINY COWBIRDS AND YELLOW-SHOULDERED BLACKBIRDS IN PUERTO RICO

Two significant breeding populations of the Yellow-shouldered Blackbird remain in Puerto Rico: (1) SW Puerto Rico, in a narrow coastal zone about 35 km long, from Guánica to Boca Prieta and (2) E Puerto Rico, on Roosevelt Roads Naval Station, near Ceiba. Small, isolated populations exist outside these


The Condor 79:176–184, 1977

two main centers, notably at San Germán, where we found 6 nests. We estimate that about 2,000 Yellow-shouldered Blackbirds remain in SW Puerto Rico, 200 in E Puerto Rico and 200 on Mona Is. The Shiny Cowbird is distributed throughout Puerto Rico, but is most common in disturbed lowland habitats. Roost counts (table 1) indicate that the cowbird now outnumbers the Yellow-shouldered Blackbird. The seasonal distribution of the Shiny Cowbird is not fully understood, but roost counts show that cowbirds move into the SW coastal zone during June–September. Few cowbirds remain on the SW coast after October, and it is possible that they move to the N coast or to the interior. For example, we recorded 1,175 Shiny Cowbirds at an inland roost, in San Germán, on 12 February 1975. Concentration of cowbirds on the SW coast in the summer coincides with the breeding season of the Yellow-shouldered Blackbird and most other passerine species there.

TABLE 1. Seasonal variation in composition of a communal blackbird roost near La Parguera, Puerto Rico.

| Date | Yellow-shouldered Blackbird | Shiny Cowbird | Greater Antillean Grackle |
|---|---|---|---|
| 19 Feb 73 | 232 (89%) | 2 (1%) | 27 (10%) |
| 3 May 73 | 1074 (87%) | 60 (5%) | 100 ( 8%) |
| 14 Jun 73 | 1411 (51%) | 814 (30%) | 517 (19%) |
| 17 Jun 73 | 1501 (35%) | 2175 (51%) | 586 (14%) |
| 7 Sep 73 | 1663 (27%) | 4299 (70%) | 209 ( 3%) |

## BREEDING SEASONS

In La Parguera the first Yellow-shouldered Blackbird nest with eggs was found on 2 June, and the last complete clutch on 8 September. At Ceiba the blackbird's breeding season starts about a month earlier than at La Parguera, the first Ceiba eggs being found on 1 May and the last complete clutch on 24 June. The later onset of Yellow-shouldered Blackbird breeding at La Parguera correlates with the later start of fall rains there. In San Germán, in interior SW Puerto Rico, blackbirds were nesting as early as 17 May. In San Germán, on 24 May 1975, we captured an immature blackbird that probably had fledged in mid-April. Since the Yellow-shouldered Blackbird acted as the main host of the Shiny Cowbird in the areas we visited, the cowbird's breeding season corresponded to that of the blackbird. However, we found one cowbird egg lying on the ground on 7 May 1975 at La Parguera, about a month before the earliest Yellow-shouldered Blackbird eggs were found there that year.

## BREEDING HABITATS AND NEST SITES

At La Parguera we found 23 Yellow-shouldered Blackbird nests on small offshore red mangrove (*Rhizophora mangle*) cays. These nesting islands were usually less than 1,000 m², and were 250–550 m offshore. Open cup nests, typical of *Agelaius*, were built on main branches or on trunks 0.2–4.0 m above the water. Only 3 of the 19 offshore nests contained cowbird eggs. Although cowbirds often roosted on the offshore cays with other icterids, they seldom visited these sites during the day.

At both La Parguera and Ceiba, blackbirds nested in mainland mangroves (54 nests), mainly black mangroves (*Avicennia germinans*). They placed their open nests on mangrove crotches 0.4–4.5 m above the ground or water. They also built nests in hollow stumps or in holes in dead mangroves. The greatest depth of a cavity nest was 23 cm, and we found eggs as low as 14 cm above the ground. Entrances to cavities were as small as 4 × 8 cm (photographs in Post and Wiley 1976). Along the edge of the mangroves, the blackbirds nested in deciduous trees, mainly oxhorn bucida (*Bucida buceras*) growing in pastures. Seven nests in pastures were 4.3–6.8 m above the ground, usually placed on crotches near the end of branches.

## EGG CHARACTERISTICS

Eggs of the Shiny Cowbird are smaller than those of the Yellow-shouldered Blackbird. The mean length of 33 cowbird eggs from 17 nests was 20.3 mm, standard deviation ± 0.8 mm; the mean width was 16.7, SD ± 0.5 mm. The mean length of 20 blackbird eggs from 10 nests was 22.8 ± 1.7 mm; mean width: 17.1 ± 0.6 mm. All 161 cowbird eggs that we found were speckled with reddish-brown. The amount of speckling varied from egg to egg, but was uniformly distributed over the egg. The blackbirds' eggs were also speckled, but the purplish-brown markings were more heavily concentrated at one end than were the marks on cowbird eggs. Of the 26 cowbird eggs for which we recorded background colors, 24 were white, while 2 were light blue, which is close to the background color of the blackbird's eggs. Cowbird eggs with blue backgrounds were quite similar to the Yellow-shouldered Blackbird eggs, but the majority of the cowbird eggs (those with white backgrounds) were easily differentiated from the blackbirds'.

TABLE 2. Reproductive success of Yellow-shouldered Blackbirds and Shiny Cowbirds in Puerto Rico. Includes some nests whose histories may be incomplete.

| Species and Component | Mainland Nests | | | Offshore Nests | |
|---|---|---|---|---|---|
| | La Parguera 1975 | Ceiba 1975 | Both | La Parguera 1973–1975 | All Nests |
| Yellow-shouldered Blackbird | | | | | |
| Nest success[a] | 0.40(14/35) | 0.17(3/18) | 0.32(17/53) | 0.58(11/19) | 0.39(27/72) |
| Fledglings/nest | 0.77(27/35) | 0.17(3/18) | 0.57(30/53) | 0.89(17/19) | 0.65(47/72) |
| Fledgling/egg | 0.30(27/91) | 0.10(3/29) | 0.25(30/120) | 0.33(16/49) | 0.27(46/167) |
| Fledgling/nestling | 0.79(27/34) | 0.50(3/6) | 0.75(30/40) | 0.67(16/24) | 0.72(46/64) |
| Egg hatched/egg laid | 0.37(34/91) | 0.21(6/29) | 0.33(40/120) | 0.50(24/49) | 0.38(64/169) |
| Eggs/nest | 2.60(91/35) | 1.61(29/18) | 2.26(120/53) | 2.58(49/19) | 2.34(169/72) |
| Shiny Cowbird | | | | | |
| Nest success | 0.43(15/35) | 0.50(9/18) | 0.45(24/53) | 0.33(1/3) | 0.45(25/56) |
| Fledglings/nest | 0.69(24/35) | 0.94(17/18) | 0.77(41/53) | 0.33(1/3) | 0.75(42/56) |
| Fledgling/egg | 0.26(24/91) | 0.24(17/70) | 0.25(41/161) | 0.33(1/3) | 0.26(42/164) |
| Fledgling/nestling | 0.62(24/39) | 0.85(17/20) | 0.69(41/59) | 1.00(1/1) | 0.70(42/60) |
| Egg hatched/egg laid | 0.43(39/91) | 0.29(20/70) | 0.37(59/161) | 0.33(1/3) | 0.37(60/164) |
| Eggs/nest | 2.60(91/35) | 3.89(70/18) | 3.04(161/53) | 1.00(3/3) | 2.93(163/56) |

[a] Proportion of nests fledging at least one young.

## REPRODUCTIVE SUCCESS OF YELLOW-SHOULDERED BLACKBIRDS AND SHINY COWBIRDS

On the mainland in 1975 all 53 Yellow-shouldered Blackbird nests that we examined (35 at La Parguera and 18 at Ceiba) were parasitized by Shiny Cowbirds. In contrast, of 19 offshore nests found at La Parguera, during 1972–1975, only 3 had cowbird eggs. We may compare the reproduction of offshore nests and mainland nests to assess the impact of brood parasitism on blackbird production; such a comparison is possible because depredation due to factors other than cowbirds did not differ between habitats. Data from a sample of 54 nests at La Parguera for which we have unequivocal information show that 31.4% of 35 mainland nests were destroyed by predators, in contrast to 26.3% of 19 offshore nests. The difference is not significant.

A comparison between the reproductive success of offshore and mainland blackbird nests at La Parguera (table 2) does not reveal significant differences in any of the variables considered, although the data reveal a trend toward greater success for offshore nests in the component eggs hatched/laid. For Yellow-shouldered Blackbirds, the overall lack of difference in production between habitats, in spite of the much higher incidence of cowbird parasitism on the mainland, is probably due to two factors. First, production estimates from mainland Yellow-shouldered Blackbird nests at La Parguera (table 2) include data on cavity-nesting birds, which enjoyed significantly greater success than did blackbirds nesting in the open in the same locality and habitat (table 3). Shiny Cowbird eggs laid in cavities were also more successful. The second factor that may reduce the reproductive output of offshore blackbird nests is the long distances that the adults flew to obtain food for themselves and their nestlings: island-nesting blackbirds often visited mainland feeding sites as far as 2 km away. The delivery rate per hour per offshore nest (11.3) was significantly lower (anova; $P < .001$) than the comparable mainland rate (15.2).

In spite of the depressed feeding rates of offshore-nesting Yellow-shouldered Blackbirds, a comparison between only open nests with or without cowbird eggs (table 4) reveals a trend toward increased success for nests without cowbirds, and a significant difference in nest success. This comparison also indicates that parasitism by cowbirds reduced the production of the Yellow-shouldered Blackbird by about 0.15 fledglings/egg. Adjusting for the slightly lower number of eggs found in parasitized nests, cowbird parasitism reduced the number of Yellow-shouldered Blackbird fledglings/nest by about 0.39.

At Ceiba the average number of Shiny Cowbird eggs per nest was greater than at La Parguera (table 2), and more intense parasitism by cowbirds was correlated with lowered production of blackbirds. Conversely, Ceiba cowbirds were more successful than La Parguera cowbirds. The high success of the Shiny Cowbird at Ceiba is shown by the production of 17 fledgling cowbirds from 18 nests, while the same 18 nests produced only 3 blackbirds. In contrast, at La Parguera the number of fledglings produced by 35 nests was nearly balanced between 27 blackbirds and 24 cowbirds. One variable of cowbird

TABLE 3. Reproductive success of Yellow-shouldered Blackbirds and Shiny Cowbirds placing their eggs in cavities or in the open.[a]

| | Yellow-shouldered Blackbird | | | Shiny Cowbird | | |
|---|---|---|---|---|---|---|
| Component | Cavity nests | | Nests in the open | Cavity nests | | Nests in the open |
| Nest success | 0.86(6/7) | *[b] | 0.27(6/22) | 0.71(5/7) | | 0.36(8/22) |
| Fledglings/nest | 1.71(12/7) | | 0.50(11/22) | 1.57(11/7) | | 0.50(11/22) |
| Fledgling/egg | 0.63(12/19) | * | 0.19(11/57) | 0.52(11/21) | * | 0.19(11/59) |
| Fledgling/nestling | 0.86(12/14) | | 0.69(11/16) | 0.65(11/17) | | 0.55(11/20) |
| Egg hatched/egg laid | 0.74(14/19) | * | 0.28(16/57) | 0.81(17/21) | * | 0.34(20/59) |
| Egg/nest | 2.71(19/7) | | 2.59(57/22) | 3.00(21/7) | | 2.68(59/22) |

[a] All nests located in mainland mangroves at La Parguera, 1975.
[b] An asterisk between two values: $P < .05$ that difference is due to chance (nest success: Fisher Exact Probability Test; all others: $\chi^2$).

production, hatching success, was lower at Ceiba than at La Parguera, presumably due to the cowbirds' behavior of puncturing eggs of their own species as well as those of their hosts.

## COMPARISON WITH OTHER STUDIES

The impact of Shiny Cowbirds on Yellow-shouldered Blackbird production, shown by differences between parasitized and unparasitized nests in the number of fledglings per nest and fledglings per egg (table 4), was less than that found by King (1973) for Shiny Cowbirds parasitizing Rufous-collared Sparrows at Horco Molle, Argentina. Puerto Rican Shiny Cowbird parasitism had its main effect during the egg stage of the Yellow-shouldered Blackbird, but in Argentina, the Shiny Cowbird had a greater impact during the nestling stage. Nestling Rufous-collared Sparrows starved in the face of cowbird competition. This difference in host response reflects the size difference of the two hosts. The pre-fledgling asymptotic (day 10) weight of 8 Rufous-collared Sparrows was 15.9 g, and for 6 *M. b. bonariensis*, 31.3 g (King 1973). Mean weight at time of fledging (day 13–15) for 10 Yellow-shouldered Blackbirds was 30.4 g, and for 23 *M. b. minimus*, 27.5 g. Once hatched, nestling blackbirds were able to compete with nestling cowbirds (fig. 1). However, at Ceiba the relative lack of Yellow-shouldered Blackbird nestling mortality was outweighed by higher egg loss, and fewer host young fledged per nest than in two South American studies of the Rufous-collared Sparrow (Hoy and Ottow 1964, King 1973).

The nest success of the Shiny Cowbird was about the same for the two Puerto Rican and two South American study sites although both Puerto Rican cowbird populations had lower hatching success than did either South American population (table 2; King 1973, table 1). Components of cowbird production at La Parguera are similar to those for both South American studies, although La Parguera cowbirds achieved similar success in fledglings/nest with a greater output of eggs/nest. At Ceiba cowbirds laid more eggs/nest, and although they were less successful than all other populations in the proportion of eggs hatched, greater egg output presumably enabled Ceiba cowbirds to achieve the greatest success in fledglings/nest of any of the four study sites. The La Parguera, Horco Molle and Rio de Janeiro populations of Shiny Cowbirds had a per nest success similar to their hosts, but cowbird production at Ceiba heavily outweighed host production.

King (1973) hypothesized that the Rufous-collared Sparrow reduced its nest load to correspond to the equivalent of 3.50 sparrows or 1.75 cowbirds. Under conditions of food shortage, such reduction in brood size improves the chances of survival of older nestlings, and parental feeding effort is not squandered on doomed young. Reduction in brood size occurs during the egg stage or early nestling stage, reduction during the latter stage being facilitated by the size differences of asynchronously hatching young often found in cowbird-parasitized nests (fig. 1). King presented data showing that the number of Shiny Cowbird eggs was reduced by about 28% and the number of Rufous-collared Sparrow eggs by about 33% during the incubation

TABLE 4. Reproductive success of Yellow-shouldered Blackbirds using open nests around La Parguera.

| Component | Parasitized by cowbirds[a] | | Not parasitized by cowbirds[b] |
|---|---|---|---|
| Nest success | 0.30(9/30) | *[c] | 0.63(10/16) |
| Fledglings/nest | 0.53(16/30) | | 0.94(15/16) |
| Fledgling/egg | 0.21(16/76) | | 0.36(15/42) |
| Fledgling/nestling | 0.67(16/24) | | 0.75(15/20) |
| Egg hatched/egg laid | 0.32(24/76) | | 0.48(20/42) |
| Eggs/nest | 2.53(76/30) | | 2.63(42/16) |

[a] 27 nests on mainland; 3 offshore.
[b] All offshore nests.
[c] An asterisk between two values: $P < .05$ that difference is due to chance.

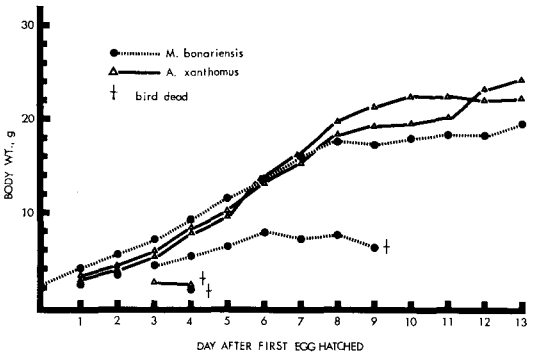


FIGURE 1. Growth rates of six nestlings contained in one Yellow-shouldered Blackbird nest at La Parguera, 1975.

period. He felt that brood reduction by the sparrow may be an adaptation that enables it to maintain its productivity while being parasitized by cowbirds. A difficulty with interpreting brood reduction data such as King's is in deciding whether the host or a cowbird removed eggs, or whether the host removed cowbird-damaged eggs.

Our data give no indication of brood reduction by *A. xanthomus* (table 5). In all cases except one, differences between final number of eggs laid, and number of eggs hatched were due to hatching failure, which we could confirm, as eggs remained in the nest. Hatching failure may result from the inability of the female Yellow-shouldered Blackbird to properly incubate or turn a large number of eggs.

Average nest load at time of hatching was 2.30 blackbirds and 2.30 cowbirds, which represents an average reduction of 0.30 blackbird eggs, but an increase of 0.20 cowbird eggs. King (1973) found that brood reduction in Rufous-collared Sparrow nests was 0.66 eggs for both species. Our data indicate that the Yellow-shouldered Blackbird does not practice adaptive brood reduction: its losses occur during the nestling state (fig. 1), and are thus maladaptive.

## EGG-PUNCTURING

Egg-puncturing by Shiny Cowbirds was the main cause of reproductive failure at Ceiba, and we attribute the large difference in Yellow-shouldered Blackbird production between La Parguera and Ceiba to egg loss (table 2). We found 29 cowbird and 20 blackbird eggs punctured in 12 of 18 nests at Ceiba. At La Parguera we found only one punctured egg in the 38 blackbird nests that were parasitized, and we have no evidence that La Parguera cowbirds or blackbirds were removing punctured eggs. Also, the mean number of blackbird eggs was about the same for parasitized and unparasitized nests (table 4).

TABLE 5. Clutch size histories of cowbird-parasitized Yellow-shouldered Blackbird nests whose complete histories are known, La Parguera, 1975.

| No. of Eggs | | | | | |
|---|---|---|---|---|---|
| Initial | | Final[a] | | Birds hatched | |
| Blackbird | Cowbird | Blackbird | Cowbird | Blackbird | Cowbird |
| 3 | 3 | 3 | 3 | 3 | 3 |
| 3 | 3 | 3 | 3 | 3 | 3 |
| 3 | 2 | 3 | 2 | 2[b] | 1[b] |
| 3 | 3 | 2 | 3 | 2 | 2[b] |
| 3 | 3 | 1[c] | 5 | 0 | 2 |
| 3 | 2 | 3 | 2 | 3 | 1[b] |
| 3 | 2 | 3 | 2 | 3 | 2 |
| 3 | 5 | 3 | 5 | 3 | 5 |
| 3 | 3 | 3 | 3 | 3 | 2 |
| 3 | 3 | 3 | 3 | 1[b] | 2 |
| Means | | | | | |
| 3.00 | 2.90 | 2.70 | 3.10 | 2.30 | 2.30 |

[a] At time first egg hatched.
[b] Differences were not due to egg removal; unhatched eggs were still in nest.
[c] Cowbirds were presumably adding and removing eggs throughout incubation period.

The difference in egg-puncturing behavior of the two cowbird populations could be due to several factors. First, the Shiny Cowbird has been in E Puerto Rico at least 10 years longer than in W Puerto Rico, where it only arrived about 1969 (Post and Wiley 1977). Gene flow may be restricted as the Shiny Cowbird continues to move westward, and egg-puncturing could be rare in W Puerto Rico due to the reduced genetic variation there. After its appearance in the population, the egg-puncturing trait may be exhibited by only a few individuals and then may spread gradually by local enhancement (Hinde 1970: 582).

Secondly, indiscriminate egg-puncturing may appear only as a consequence of high parasite density combined with low host density. The greater amount of egg-puncturing at Ceiba is correlated with the greater intensity of brood parasitism there. The average cowbird clutch size at Ceiba (3.9, SE ± 0.4) was significantly larger than at La Parguera (2.9 ± 0.3). Experiments with Brown-headed Cowbirds (*Molothrus ater*) show that females of that species prefer not to lay in nests containing too few or too many eggs (A. King, pers. comm.). Instead of avoiding nests containing too many eggs, the "stronger and more vigorous" (Selander 1964) Shiny Cowbird may indiscriminately puncture eggs. Female Shiny Cowbirds may act spitefully (Hamilton 1970) if they are ready to lay but

TABLE 6. Incidence of brood parasitism by Shiny Cowbirds in mainland habitats of coastal Puerto Rico.

| Species | 1975 | | | | 1976 | |
|---|---|---|---|---|---|---|
| | La Parguera | | Ceiba | | Ceiba | |
| | Number of nests examined | Number of nests containing Shiny Cowbird eggs | Number of nests examined | Number of nests containing Shiny Cowbird eggs | Number of nests examined | Number of nests containing Shiny Cowbird eggs |
| Gray Kingbird (*Tyrannus dominicensis*) | 2 | 0 | 26 | 0 | 10 | 1 |
| Northern Mockingbird (*Mimus polyglottos*) | 1 | 0 | 2 | 0 | – | – |
| Pearly-eyed Thrasher (*Margarops fuscatus*) | – | – | 3 | 0 | 6 | 0 |
| Red-legged Thrush (*Turdus plumbeus*) | – | – | 1 | 0 | – | – |
| Yellow Warbler (*Dendroica petechia*) | 3 | 0 | 11 | 0 | 8 | 2 |
| Bananaquit (*Coereba flaveola*) | 2 | 0 | 11 | 0 | 6 | 0 |
| Greater Antillean Grackle (*Quiscalus niger*) | 5 | 0 | 9 | 0 | 1 | 1 |
| Yellow-shouldered Blackbird (*Agelaius xanthomus*) | 35 | 35 | 18 | 18 | 8 | 8 |
| Bronze Mannikin (*Lonchura cucullata*) | – | – | – | – | 3 | 1 |

only encounter nests with too many eggs, and their egg destruction would be exacerbated by multiple cowbird visits. Hoy and Ottow (1964) felt that Shiny Cowbird egg-puncturing is more of a general habit than an adaptation for parasitism; they observed males as well as females puncture eggs. That egg-puncturing may involve spite is indicated by eight Ceiba nests we found with all cowbird and blackbird eggs punctured: either female cowbirds had punctured the eggs and did not lay others, or males did the puncturing.

During the egg-laying or early incubation period, many passerine species, including Yellow-shouldered Blackbirds, desert nests which contain damaged eggs. To achieve synchronization with hosts, the cowbird must lay its eggs during an early stage of the host nest, and the female cowbird should usually remove punctured eggs to reduce the risk of host desertion. The large number of punctured eggs we found in nests at Ceiba supports our hypothesis that the number of parasites is too large for the host population, resulting in the appearance of indiscriminate egg-puncturing. Locally, such an imbalance in parasite and host numbers may occur more often than reported. In Argentina, Hoy and Ottow (1964) discovered a group of about 20 nests of the Chestnut-capped Blackbird (*Agelaius ruficapillus*) which they believed had been abandoned because of excessive parasitism by Shiny Cowbirds. The colony contained many broken *A. ruficapillus* eggs and 94 cowbird eggs, "nearly all unsuccessful." The intense parasitism shown by some populations of the Shiny Cowbird may be related to the species' tendency toward host specificity.

## HOST PREFERENCE

We found Shiny Cowbirds parasitizing mainly Yellow-shouldered Blackbirds. In the same habitats and at the same time of year that female Shiny Cowbirds were laying eggs in Yellow-shouldered Blackbird nests, we examined 110 nests containing eggs of eight other passerine species and found cowbird eggs in only five of these nests (table 6). Few data are available on host preference, since most reports say nothing of nests that do not contain cowbird eggs. Most information on Shiny Cowbird parasitism has been a by-product of studies of other species, and little effort has been made to search extensively for additional hosts of the cowbirds. In spite of these limitations, several studies from South America suggest that locally the Shiny Cowbird prefers one host species over others. Sick (1958) in coastal Brazil found that of 95 Rufous-collared Sparrow nests, 57 (60%) were parasitized by Shiny Cowbirds, but only 2 of 33 nests of 9 other species contained cowbird eggs. Johnson (1967:330) reported from Chile that of a total of 72 parasitized nests, 44 were of the Common Diuca

Finch (*Diuca diuca*), and the remaining 28 of 7 other species. Friedmann and Smith (1955) reported "exclusive use" of the Greater Antillean Grackle (*Quiscalus niger*) by Shiny Cowbirds, but they did not give the number of nests parasitized nor indicate other species' nests examined. To our knowledge, there are no known cases of Shiny Cowbirds parasitizing all the nests of one host throughout a whole breeding season, such as we found on mainland Puerto Rico.

The Shiny Cowbird's preference for the Yellow-shouldered Blackbird may be due to the following combination of factors: (1) Behavior of an expanding population. Cowbirds who arrive in a new region may concentrate on the first suitable host whom they encounter. Such preference may reduce the risk that females have in entering additional unfamiliar habitats or nest sites. Hamilton and Orians (1965) pointed out that the best strategy for a female brood parasite is to time her ovulation to the events of a specific host nest, and then to do the best she can with subsequent eggs. After parasitizing their target nests, female Shiny Cowbirds may lay subsequent eggs in nearby nests already containing many eggs. (2) Taxonomic relationship of host and parasite. *Agelaius* and *Molothrus* are closely related, and we would expect brood parasitism to be more prevalent between related species than between unrelated (Hamilton and Orians 1965). In South America, *Agelaius* spp. are frequent hosts of Shiny Cowbirds. (3) Egg similarity. The eggs of the Yellow-shouldered Blackbird and the Shiny Cowbird are similar in size and color. Such resemblance may act as a stimulus to egg-laying by female cowbirds. (4) Lack of crypticity of the blackbird nests. The open nests of the Yellow-shouldered Blackbird are often placed in exposed sites; they are bulkily constructed of debris such as plastic bags, colored string and brightly colored algae. Such nests would be easily found by cowbirds. (5) Colonial nesting pattern of the Yellow-shouldered Blackbird. Nests are usually close together, occasionally as close as 3.5 m. Proximity of breeding pairs would enable female cowbirds to find sufficient nests with minimal energy expenditure. (6) Nest attendance. Yellow-shouldered Blackbird adults defend only a small area around their nests, and spend long periods feeding away from the breeding areas. These behaviors would allow cowbirds easy access to blackbird nests. (7) Ecological similarities. Both species feed in mixed flocks around cattle feeding lots, monkey feeders and pastures. Both roost together at night and in secondary roosts during the day. Year-around association of parasite and host increases the probability of synchronized breeding season.

## BROOD PARASITISM AND POPULATION MAINTENANCE OF THE YELLOW-SHOULDERED BLACKBIRD

Like other tropical passerines whose survival has been studied (see for example Snow 1962, Snow and Lill 1974), the Yellow-shouldered Blackbird is relatively long-lived. The minimum annual survival of 250 adult Yellow-shouldered Blackbirds that were color-marked around La Parguera was 82.4%. The survival to adulthood of 29 color-marked juveniles was 65.5%, while 27.6% of 29 color-marked fledglings survived to become juveniles (Post, unpubl. data). The annual recruitment rate, 18.1% (the product of the latter two percentages), is equal to the annual adult mortality, meaning that about two Yellow-shouldered Blackbirds must be fledged per breeding pair each year for the population to be maintained. Production at La Parguera (table 2) is below that needed for population maintenance. Although our survival data are for La Parguera, we may reasonably assume that once they have fledged, Yellow-shouldered Blackbirds at Ceiba have about the same survival rate. Production at Ceiba was far below that required for population maintenance. Because we do not have information on the success of unparasitized nests at Ceiba, we cannot judge to what extent this is due to brood parasitism. But the fact that only three Yellow-shouldered Blackbirds were produced by 18 nests in 1975, and none from 8 nests in 1976, strongly implies that the low level of Yellow-shouldered Blackbird production at Ceiba is related to brood parasitism by Shiny Cowbirds.

The Barbados race of the Yellow Warbler (*Dendroica p. petechia*) is believed to have become rare due to brood parasitism by the Shiny Cowbird (Bond 1966), and the Kirtland's Warbler (*D. kirtlandii*) has declined due to severe brood parasitism by *Molothrus ater* (Mayfield 1973). In some respects the relationship of the Shiny Cowbird and the Yellow-shouldered Blackbird resembles that of the Brown-headed Cowbird and the Kirtland's Warbler. Both hosts apparently lack defenses against cowbirds, and both host populations are small, but heavily parasitized by cowbirds. Incidence of cowbird parasitism was 60–70% for the Kirtland's Warbler (Mayfield 1973) vs. 80% for the Yellow-shouldered Blackbird. Small popula-

tions may be particularly sensitive to cowbird parasitism because when main host numbers are low, the parasite does not respond by switching to alternate hosts. But unlike the Kirtland's Warbler, the Yellow-shouldered Blackbird still has some nesting habitat free from cowbirds: the offshore cays around La Parguera. Also, the blackbird occasionally nests in cavities, and although parasitized by cowbirds, these nests have relatively high success. Offshore- and cavity-nesting may enable remnant Yellow-shouldered Blackbird populations to maintain themselves for a sufficient period to evolve some defenses against brood parasitism, such as egg rejection (operating against the evolution of such behavior, however, is the reduced genetic variation of these small populations). But egg rejection, if it appears, has a high selection coefficient and may become fixed rapidly (Rothstein 1975a). Although no other species of *Agelaius* is known to be a rejecter, as defined by Rothstein (1975b), neither has any member of the genus been known to have been subjected to such severe selective pressure due to brood parasitism as has *A. xanthomus*.

## SUMMARY

During four breeding seasons we studied the reproductive relationships of a brood parasite, the Shiny Cowbird (*Molothrus bonariensis*) and the Yellow-shouldered Blackbird (*Agelaius xanthomus*), its main host in coastal Puerto Rico. At one study site, in E Puerto Rico, all 26 Yellow-shouldered Blackbird nests were parasitized, while at the other study site, in SW Puerto Rico, 38 of 54 blackbird nests had cowbird eggs. Lack of parasitism was due to habitat preferences of cowbirds, and there was no seasonal variation in the incidence of parasitism of the blackbirds. Cowbirds parasitized only 5 of 110 nests of other passerines nesting in the same habitats at the same time as the blackbirds.

In SW Puerto Rico, cowbird brood parasitism reduced the reproductive output of Yellow-shouldered Blackbirds by about 0.39 fledglings per nest. In E Puerto Rico the effect of brood parasitism appeared to be more severe than in the SW, this difference being related to the greater intensity of cowbird parasitism in the former region. In the SW, cowbird and blackbird production was nearly balanced: 35 nests produced 27 blackbirds and 24 cowbirds; in the E, 18 nests produced only 3 blackbirds, but 17 cowbirds. In the E, most blackbird nest losses occurred during the egg stage, due to egg-puncturing by cowbirds. This behavior was rare in SW Puerto Rico.

Compared to the effect of the Shiny Cowbird on its main South American host, the Rufous-collared Sparrow (*Zonotrichia capensis*), cowbird parasitism in SW Puerto Rico caused a lesser reduction in Yellow-shouldered Blackbird reproductive output. Yellow-shouldered Blackbird nestlings are larger than Shiny Cowbird nestlings, and thus are at less competitive disadvantage than is the Rufous-collared Sparrow toward the Shiny Cowbird.

The preference shown by Shiny Cowbirds for Yellow-shouldered Blackbird nests is thought to be a behavioral result of an expanding parasite population, in combination with features of the blackbird's biology which predispose it to brood parasitism. Reproductive data from one breeding season and survival data collected during three years indicate that the Yellow-shouldered Blackbird population may not be maintaining itself, in part due to cowbird brood parasitism. Other populations of brood parasites have had similar effects on new hosts.

## ACKNOWLEDGMENTS

We thank the Caribbean Primate Research Center for allowing access to their facilities and for providing boats and equipment. We thank F. A. Enders and J. S. Greenlaw for criticizing the manuscript. We were aided in the field by M. M. Browne, B. Wiley, and K. S. Wilson. While conducting research at La Parguera, Post was supported by N.I.M.H. grant No. DA-00700; principal investigator, J. G. Vandenbergh.

## LITERATURE CITED

Bond, J. 1966. Eleventh supplement to the Checklist of the birds of the West Indies (1956). Acad. Nat. Sci. Philadelphia: 1–13.

Bond, J. 1973. Eighteenth supplement to the Checklist of the birds of the West Indies (1956). Acad. Nat. Sci. Philadelphia: 1–12.

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

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233.

Friedmann, H., and F. D. Smith, Jr. 1955. A further contribution to the ornithology of northeastern Venezuela. U.S. Natl. Mus. Proc. 104: 463–524.

Grayce, R. L. 1957. Range extensions in Puerto Rico. Auk 74:106.

Hamilton, W. D. 1970. Selfish and spiteful behaviour in an evolutionary model. Nature 228: 1218–1220.

Hamilton, W. J. III, and G. H. Orians. 1965. Evolution of brood parasitism in altricial birds. Condor 67:361–382.

Hinde, R. A. 1970. Animal behaviour. McGraw-Hill Book Co., New York.

Hoy, G. and J. Ottow. 1964. Biological and

oölogical studies of the molothrine cowbirds (Icteridae) of Argentina. Auk 81:186–203.

HUDSON, W. H. 1920. The birds of La Plata. J. M. Dent and Sons, Ltd. London.

JOHNSON, A. W. 1967. The birds of Chile. Platt Establecimientos Gráficos S.A., Buenos Aires.

KING, J. R. 1973. Reproductive relationships of the Rufous-collared Sparrow and the Shiny Cowbird. Auk 90:19–34.

MAYFIELD, H. F. 1973. Census of Kirtland's Warbler in 1972. Auk 90:684–685.

NEWTON, A. 1860. To the editor of 'The Ibis' [letter]. Ibis 2:307–308.

POST, W. AND J. W. WILEY. 1976. The Yellow-shouldered Blackbird—present and future. Am. Birds 30:13–20.

POST, W. AND J. W. WILEY. 1977. The Shiny Cowbird in the West Indies. Condor 79:119–121.

ROTHSTEIN, S. I. 1975a. Evolutionary rates and host defenses against avian brood parasitism. Am. Nat. 109:161–176.

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

SELANDER, R. K. 1964. Behavior of captive South American cowbirds. Auk 81:394–402.

SICK, H. 1958. Notas biológicas sôbre o gaudério, *"Molothrus bonariensis"* (Gmelin) (Icteridae, Aves) Rev. Bras. Biol. 18:417–431.

SICK, H. AND J. OTTOW. 1958. Vom brasilianischen Kuhvogel, *Molothrus bonariensis*, und seinen Wirten, besonders dem Ammerfinken, *Zonotrichia capensis*. Bonn. Zool. Beitr. Heft 1/9:40–62.

SNOW, D. W. 1962. A field study of the Black and White Manakin, *Manacus manacus*, in Trinidad. Zoologica 47:65–104.

SNOW, D. W. AND A. LILL. 1974. Longevity records for some neotropical land birds. Condor 76: 262–267.

*Research Division, N.C. Dept. of Mental Health, Raleigh, N.C. Address of second author: Institute of Tropical Forestry, U.S. Forest Service, Box 21, Palmer, Puerto Rico 00721. For reprints write: W. Post, c/o Biology Dept., C.W. Post Center of L.I. Univ., Greenvale, N.Y. 11548.* Accepted for publication 27 December 1976.