

THE DECLINE OF AN ADAPTATION IN THE ABSENCE OF A PRESUMED SELECTION PRESSURE

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Abstract.—The colonial nesting Village Weaver (*Ploceus cucullatus*) lays eggs that vary in ground color and pattern, but individual females lay similar eggs each time. Tests on captive African stocks have shown that females reject eggs of other cohorts if such eggs are sufficiently different. The Village Weaver may have evolved rejection behavior and variable eggs in response to cuckoo parasitism in Africa. The Village Weaver was introduced into Hispaniola from Africa as early as the 18th century. Before the arrival of the Shiny Cowbird (*Molothrus bonariensis*) in the early 1970's, there were no brood parasites on Hispaniola. Furthermore, in an experimental parasitism study, Hispaniolan Village Weavers accepted both dummy eggs and dissimilar Village Weaver eggs. The Village Weaver may have decreased the egg-rejection behavior in the absence of the selective pressure of brood parasitism. Now Hispaniolan populations of the Village Weaver are parasitized by the Shiny Cowbird, which lays eggs dissimilar to those of the weaver. Brood parasitism by the Shiny Cowbird exerts a detrimental impact on the Village Weaver by reducing nest success and productivity.

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Few documented cases of evolutionary change within historic times have been reported, and such cases generally involve the development of a new adaptation in response to a new selective pressure. Here, we report a case involving the decline of a discrete adaptation in response to removal of a selection pressure: a decrease of egg-ejection behavior in the Village Weaver (*Ploceus cucullatus*) in the absence of brood parasitism.

The Village Weaver is a polygynous, colonial-nesting species endemic to the sub-Saharan region of Africa (Crook, 1963; Collias and Collias, 1970, 1971). The eggs laid by this species vary in ground color and pattern of spotting among females, but egg pigmentation is constant for individuals (Victoria, 1972; Collias, 1984). Victoria (1972) found that an individual female could recognize her own egg type and would eject from her nest foreign eggs differing markedly from her own. The incidence of egg rejection was proportional to the degree of difference between the eggs. Victoria (1972) and Collias (1984) postulated that the Vil-

lage Weaver evolved rejection behavior in response to interspecific brood parasitism by the Didric Cuckoo (*Chrysococcyx caprius*).

The Village Weaver was introduced into Hispaniola from Africa as early as the 18th century (De Saint-Mery, 1797). De Saint-Mery indicated that the population may have originated from escapees from aviaries maintained at that time. Wetmore and Swales (1931) and Bond (1936) believed that the weaver was probably introduced at the time slave ships were plying between Africa and the West Indies. From the point of introduction in Haiti, weavers spread eastward to the Dominican Republic. The species is now common in lowland areas throughout the island and in some locales has become a serious agricultural pest (Fitzwater, 1971; Dod, 1978; pers. observ). The race introduced into Hispaniola conforms with *P. c. cucullatus* of western Africa (Wetmore and Swales, 1931); this race has been studied by Victoria (1972), Collias and Collias (1970, 1971), and Collias (1984).

The northern race of the Shiny Cowbird (*Molothrus bonariensis minimus*) was originally confined to South America, Trinidad, and Tobago. However, in the last 90 years

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it has spread throughout the West Indies, aided by the destruction of forests and perhaps by introductions (Bond, 1966, 1971, 1973; Ricklefs and Cox, 1972; Post and Wiley, 1977; Garrido, 1983; Cruz et al., 1985; Cruz et al., 1988). The Shiny Cowbird was first observed in Hispaniola in 1972 (Post and Wiley, 1977). From 1976 to 1978, Arendt and Vargas Mora (1984) observed cowbirds in 13 widely scattered localities in eastern and central Dominican Republic, including Saona Island (off southeastern Hispaniola). By the 1980's, the Shiny Cowbird had become established in many lowland sites throughout the island.

Before the arrival of the Shiny Cowbird in the 1970's, there were no brood parasites on Hispaniola (Post and Wiley, 1977; Arendt and Vargas Mora, 1984; Cruz et al., 1985). Hence, the Village Weaver lived in an environment free from interspecific brood parasitism for about 200 years. These circumstances provided a "natural experiment": did egg-rejection behavior remain in a population in the absence of the selective pressure of brood parasitism?

MATERIALS AND METHODS

From April to August of 1974–1978 and 1982–1985, we gathered information on the breeding biology of the Village Weaver and its interaction with the Shiny Cowbird in the southern coastal plain of the Dominican Republic, primarily at La Romana, Duverge, Santo Domingo, Cabo Rojo, and San Cristobal. Much of the region is cultivated (e.g., sugarcane, maize, rice, banana) or grazed. These modified environments are preferred by both the Village Weaver and the Shiny Cowbird, and the species were often observed feeding together. Village Weavers construct their nests in trees, and we found colonies with up to 150 nests in a single tree.

We recorded the frequency with which the Village Weaver was used as a host species, and the effects of brood parasitism on host breeding success. Each weaver nest was marked with a coded tag (inconspicuously placed). At each visit to the study areas (2–4 day intervals), we inspected host nests to determine the number of parasite eggs and chicks. Causes of nest failure were determined whenever possible. We defined

a nest as "active" when the resident laid at least one egg and as "successful" when the host fledged at least one of its own young. Nests that fledged only cowbird young were considered to have failed.

Species that eject cowbird eggs are generally not detectable unless field experiments are conducted. We followed Rothstein's (1971, 1975a, 1975b) technique of experimental parasitism, using both artificial and real cowbird and Village Weaver eggs. Eggs of the Shiny Cowbird are similar in size to those of the Village Weaver. The mean length of cowbird eggs was 20.65 ± 0.93 (SD) mm ($N = 235$); the mean width was 16.46 ± 0.59 mm ($N = 235$). The mean length of weaver eggs was 22.25 ± 0.93 mm ($N = 87$), and the mean width was 15.22 ± 0.51 mm ($N = 85$). Although Village Weaver and Shiny Cowbird eggs differ little in size, they are strikingly different in coloration. The eggs ($N = 625$) of Village Weavers in our study areas ranged in color from light blue-green (35%) to medium blue-green (47%) and dark blue-green (18%). In addition, they may be plain (37%), lightly spotted (10%), moderately spotted (41%), or heavily spotted (11%). Each female weaver consistently lays eggs of a specific color and pattern, which may be distinct from those of other females in the colony. All cowbird eggs that we found were off-white and speckled with reddish brown uniformly distributed over the egg ($N = 93$). The amount of speckling varied from egg to egg, but was usually uniformly distributed.

Real cowbird and weaver eggs were taken from nests not involved in experiments. Two weaver egg morphs were used: medium blue-green with no spotting ($N = 23$ trials), and medium blue-green with spotting ($N = 40$ trials). Artificial eggs were constructed of plastic wood dough and coated with acrylic paint. They were similar in size ($\bar{x} = \pm 2.5\%$), weight ($\bar{x} = \pm 4.2\%$), and shape to real cowbird and weaver eggs. We painted artificial weaver eggs to resemble the real-egg morphs used in the study: medium blue-green with no spotting ($N = 19$ trials) or medium blue-green with spotting ($N = 30$ trials); artificial cowbird eggs ($N = 40$ trials) were off-white and speckled with reddish brown.

We selectively placed experimental eggs in host nests during egg-laying or early (first

TABLE 1. Shiny Cowbird parasitism at the nests of five host species in areas of the Dominican Republic where the Shiny Cowbird is known to occur. Scientific names: Palmchat, *Dulus dominicus*; Black-whiskered Vireo, *Vireo altiloquus*; Yellow Warbler, *Dendroica petechia*; Black-cowled Oriole, *Icterus dominicensis*; Village Weaver, *Ploceus cucullatus*. Numbers of colonies sampled are given in parentheses.

Host species	1974-1977			1982		
	Total nests	Parasitized		Total nests	Parasitized	
		Number	%		Number	%
Palmchat	243 (24)	13	5.3	62 (6)	16	25.8
Black-whiskered Vireo	14	2	14.3	9	6	66.7
Yellow warbler	19	2	10.5	12	10	83.3
Black-cowled Oriole	24	7	29.2	6	6	100.0
Village Weaver	936 (78)	12	1.3	134 (11)	21	15.7

three days) incubation. All eggs were placed in nests in the morning to simulate the timing of natural parasitism by the cowbird (Hoy and Ottow, 1964; Cruz et al., 1985). During a single visit to each nest, one experimental egg was added and one host egg was removed. No birds were tested more than once. After nests were experimentally parasitized, they were checked within 24 hours for the response by the hosts, with subsequent checks made daily for up to five days. Birds that either ejected the experimental egg or abandoned the nests within five days following experimental parasitism were considered to be egg rejecters. Our null hypothesis was that rejection of a spotted, plain, or cowbird egg morph was independent of host egg color.

To eliminate a possible bias introduced by handling and marking the eggs, we performed 20 control tests in which the female's own eggs were removed, marked, and replaced. We also transferred cracked eggs (one per nest) into eight weaver nests to determine whether adults would respond to another form of egg change.

RESULTS

Shiny Cowbird Parasitism of the Village Weaver.—Our studies in the Dominican Republic began in 1974, just as the Shiny Cowbird arrived there. In areas where the cowbird was known to occur, 1.3% of the Village Weaver nests we observed were parasitized by cowbirds (12 of 936 nests; Table 1) between 1974 and 1977. By 1982 the incidence of cowbird parasitism on the Village Weaver had increased to 15.7% (21 of 134 nests; Table 1). Besides finding cowbird eggs and chicks in weaver nests, we have also seen Village Weavers feeding fledgling

cowbirds ($N = 8$). Additionally, we have recorded four other cowbird host species in the study areas (Table 1).

Experimental Parasitism.—We experimentally parasitized 170 Village Weaver nests by the addition of real or artificial eggs (Table 2). For females laying a particular host egg morph, the incidence of ejection was independent of whether the introduced egg was real or artificial (Table 2). Since the responses to artificial and real eggs were not statistically significant, we combined these results. Experimental eggs were rejected in only 23 of 170 (13.5%) trials. For Village Weavers laying plain eggs, the rejection rates of plain, spotted, and Shiny Cowbird eggs were 15.0%, 13.3%, and 16.7%, respectively; these rejection rates do not differ significantly (Table 2). Similarly, the rejection rate by Village Weavers laying spotted eggs was higher for plain than for spotted or cowbird eggs, but it was not statistically significant. Hence, the rejection rates of different egg morphs were independent of host egg color.

Control eggs (eggs that we removed, marked, and replaced in the same nest, $N = 20$ trials) were never rejected. Females ejected the cracked eggs that we introduced in all of eight trials; in four of these trials, the parents' own eggs were cracked and replaced. This indicates that parents are able to identify and reject at least some kinds of defective or unwanted eggs.

Egg-Rejection Behavior in African Populations of the Village Weaver.—Victoria (1972), in a series of 322 egg-replacement trials involving 27 females (captive African stock from Senegal and their aviary descendants), showed that an individual female could recognize her own egg type and would eject eggs differing markedly from her own

TABLE 2. Rejection of introduced eggs by Village Weavers in the Dominican Republic. Table entries show number of eggs rejected/number of eggs introduced; percentage rejection is shown in parentheses for subtotals and totals. H_0 : rejection rates of different egg morphs are independent of host color; $X^2 = 0.679$, $d.f. = 2$ and 2.04 for plain and spotted host-egg morphs, respectively, $P > 0.05$.

Host egg morph	Egg source	Introduced eggs			Total
		Village Weaver		Shiny Cowbird	
		Plain	Spotted		
Plain	real	1/10	2/18	1/8	4/36
	artificial	2/10	2/12	3/16	7/38
	X^2 value ($d.f.$)	0.392 (1)	0.192 (1)	0.510 (1)	
Subtotal		3/20 (15.0%)	4/30 (13.3%)	4/24 (16.7%)	11/74 (14.9%)
Spotted	real	3/13	3/22	2/10	8/45
	artificial	1/9	1/18	2/24	4/51
	X^2 value ($d.f.$)	0.512 (1)	0.718 (1)	0.952 (1)	
Subtotal		4/22 (18.2%)	4/40 (10.0%)	4/34 (11.8%)	12/96 (12.5%)
Total		7/42 (16.7%)	8/70 (11.4%)	8/58 (13.8%)	23/170 (13.5%)

from the nest (Table 3). The incidence of egg ejection was proportional to the degree of difference between the eggs. Within each color class, the chance of rejection by females that laid plain eggs was increased by the presence of spots and vice versa (Victoria, 1972). Furthermore, in 24 cases in which the host's entire clutch was removed and then replaced with dissimilar eggs, all the foreign eggs were rejected. On two occasions, a dissimilar egg was given to a female the day before she began laying her own clutch. These, too, were rejected.

Effects of Cowbird Parasitism on the Village Weaver in Hispaniola.—The Village Weaver may have reduced egg-rejection behavior in the absence of the selective pressure of brood parasitism. However, the rate of parasitism on the Village Weaver by the recently arrived Shiny Cowbird (Table 1) suggests that the cowbird is potentially a strong selective force on the Village Weaver. But how detrimental is the parasitism if the cowbird egg is accepted? We compared the reproductive success of parasitized and unparasitized Village Weaver nests (Table 4).

The nest success for unparasitized nests and that for parasitized nests did not differ significantly in 1974–1977 ($X^2 = 0.86$, $P > 0.05$) or in 1982 ($X^2 = 2.0$, $P > 0.05$). Of nests that survived to the hatching stage, 75% of parasitized nests and 89% of unparasitized nests were successful (fledged at least one weaver young) in 1974–1977 (15.7% difference; $X^2 = 1.3$, $P > 0.10$). In 1982, 67% of parasitized nests in which eggs hatched and 100% of unparasitized nests in which eggs hatched were successful (33% difference; Fisher exact probability test, $P = 0.06$). During 1974–1977, an average of 0.35 weavers fledged per egg at parasitized nests, and 0.58 weavers fledged per egg at unparasitized nests (39.7% difference; $X^2 = 6.1$, $P < 0.05$). By 1982, the mean number of fledglings produced per egg had declined to 0.23 at parasitized nests, whereas unparasitized pairs fledged an average of 0.68 weavers per egg (66.2% difference; Fisher exact probability test, $P = 0.03$). During 1974–1977, an average of 0.91 weaver chicks fledged per nest at parasitized nests, whereas unparasitized pairs fledged 1.75 per nest

TABLE 3. Rejection of introduced Village Weaver eggs by African Village Weavers (data from Victoria [1972]). Table entries show number of eggs rejected/number of eggs introduced; percentage rejection is shown in parentheses.

Host egg morphs	Introduced eggs		Total
	Plain	Spotted	
Plain	15/33 (45.5%)	49/67 (73.1%)	64/100 (64.0%)
Spotted	44/76 (57.9%)	37/146 (25.3%)	81/122 (36.5%)
Total	59/109 (54.1%)	86/213 (40.4%)	145/322 (45.0%)

TABLE 4. Reproductive success of parasitized and unparasitized Village Weaver nests, Dominican Republic. Sample sizes are given in parentheses.

Reproductive component	1974–1977		1982	
	Unparasitized nests	Parasitized nests	Unparasitized nests	Parasitized nests
Proportion of nests fledging at least one Village Weaver	0.68 (126)	0.55 (11)	0.71 (24)	0.44 (9)
Proportion of nests in which eggs hatched that fledged at least one Village Weaver	0.89 (97)	0.75 (8)	1.0 (17)	0.67 (6)
Weaver fledgling/egg	0.58 (126)	0.35 (11)	0.68 (24)	0.23 (9)
Mean \pm SD number of Shiny Cowbird eggs per Village Weaver nest	—	1.00 \pm 0.4 (12)	—	1.24 \pm 0.4 (21)
Mean \pm SD clutch size of Village Weaver	3.09 \pm 0.66 (924)	2.67 \pm 0.78 (12)	3.08 \pm 0.66 (113)	2.57 \pm 0.81 (21)
Mean \pm SD number of host chicks fledged/nest	1.75 \pm 1.42 (126)	0.91 \pm 0.94 (12)	2.00 \pm 1.45 (24)	0.67 \pm 1.00 (9)

(48% difference; Fisher-Behrens *t* test, $t = 2.80$, $d.f. = 16$, $P < 0.05$). Parasitized pairs fledged 0.67 weavers per nest and unparasitized pairs fledged 2.0 per nest in 1982 (67% difference; $t = 2.53$, $d.f. = 31$, $P < 0.05$; Table 4).

We also compared the number of Village Weaver and Shiny Cowbird eggs in parasitized and unparasitized nests (Table 4). Host clutches in parasitized nests averaged 13.6% and 16.6% fewer eggs than in nonparasitized nests in 1974–1977 and in 1982, respectively ($t = 2.19$, $d.f. = 11$; $t = 3.13$, $d.f. = 20$; both $P < 0.05$). The mean number of cowbird eggs deposited per weaver nest increased by 24% (Fisher-Behrens *t* test, $t = 2.79$, $d.f. = 20$, $P < 0.05$) between our 1974–1977 and 1982 observations.

The selective advantage of ejection behavior may be determined by using Rothstein's (1975a) equations for computation of selection coefficients. The selective advantage of ejection behavior would be proportional to the relative contribution made to the next breeding generation by birds exhibiting rejection behavior. The success rate (to fledging) of weaver eggs was 68% in unparasitized nests and 23% in parasitized nests (Table 4: 1982 data). The average clutch size was 3.08 eggs for unparasitized nests ($N = 113$ nests). Thus, the average output of weaver nests that were parasitized was 23% of 3.08 or 0.71 and that of unparasitized nests was 68% of 3.08 or 2.1 eggs. To arrive at the number of young that would

have been produced by a weaver that ejected the cowbird egg, we multiply 2.08 by 0.68. One is subtracted from the average clutch size to account for the egg the female cowbird removes (on the average); thus, a loss of one egg cannot be avoided by ejection behavior. The product of 0.68 and 2.08 is 1.41. Thus, weavers ejecting cowbird eggs would have raised an average of 1.41 young, whereas those accepting cowbird eggs raised only 0.71 or 50% as many young per nest.

DISCUSSION

Because ejection occurred at only 12% of nests tested, we consider the Village Weaver in Hispaniola to be an accepter species. However, the work done by Victoria (1972) demonstrates that acceptance of dissimilar eggs is not characteristic of the species throughout its range (Table 3). We found that weaver parents were able to identify and eject cracked eggs. Similarly, Rothstein (1982) demonstrated that accepters are responsive to egg breakage, but not to egg coloration.

Of the 22 instances of ejection, three artificial and two real eggs were found beneath the nest trees. One actual case of egg ejection was observed. An artificial egg was grasped in the bill and dropped from the nest entrance. Victoria (1972) found that the foreign weaver eggs were usually first pecked open and then ejected.

Victoria (1972) and Collias (1984) theorized that the Village Weaver evolved re-

jection behavior and variable eggs in response to parasitism by the Didric Cuckoo (*Chrysococcyx caprius*) in Africa. The Didric Cuckoo parasitizes mainly weavers (Ploceids) and is the most frequent brood parasite of the Village Weaver (Friedmann, 1948, 1968; Payne, 1967; Payne and Payne, 1967; Jensen and Vernon, 1970). There is a close agreement in egg size between the two species, and both lay a wide variety of egg types with a similar range in color and pattern. It is conceivable that egg rejection and variable eggs in the Village Weaver serve as a defense against the Didric Cuckoo, unless the cuckoo's egg to some degree matches that of the host. Payne (1967) found that various parasitic cuckoo egg morphs were found in host nests containing similar egg morphs more often than would be expected on a hypothesis of random placement. This is, however, what one would also expect to find if cuckoos laid their eggs at random and hosts removed cuckoo eggs that did not match their own. Payne's data (as reported by Rothstein [1971]) can be used to demonstrate that Didric Cuckoos do not parasitize nests in such a way that eggs laid match those of the host. Unfortunately, there have been no quantitative studies made in the field on the proportion of Didric Cuckoo eggs rejected by hosts. Victoria's (1972) study suggests that, at least in Village Weavers, this rejection does occur and with a frequency proportional to the degree of color and pattern difference between the eggs of the host and its parasites. Furthermore, it may be that the adaptive value of the Village Weaver's polytypic egg is to reduce parasitism. Certainly, the cuckoo could not evolve a specific egg mimicry, except possibly to the most common egg type. However, this may be counterbalanced by the cuckoo's tendency to lay each of her eggs in a different weaver nest (Friedmann, 1968), thus increasing the chance of matching.

Selection for Egg-Rejection Behavior.—Brood parasitism by the Shiny Cowbird has had a detrimental impact on the Village Weaver by reducing productivity. Selection might therefore favor those individuals that are able to recognize their own eggs and reject dissimilar eggs. Rothstein (1975a) suggested that rejection behavior is an evolved response to brood parasitism. If the

original Hispaniolan weaver stock was parasitized in Africa, one may assume that rejection behavior was more prevalent when weavers were first introduced. A species that evolves rejection of parasitic eggs may retain this behavior even after it ceases to be a host, because, without parasitism, its rejection may be nearly neutral in selective value (Rothstein, 1975a). This near neutrality might occur because rejection behavior does not seem to involve changes in the other behavior patterns of a species or in any aspect of the species' morphology or physiology. Therefore, the evolution of rejection behavior appears to be at no cost to other adaptations. Even more important, if a rejecter species were no longer parasitized, its rejection behavior could be manifested only under experimental conditions. Thus, any deleterious effects associated with the act of rejection would not occur naturally and, therefore, could not be selected against.

Rothstein (1975a, 1975b) has made a detailed study of egg-rejection behavior of many Brown-headed Cowbird (*M. ater*) hosts in North America. He hypothesized a rapid fixation of rejection behavior, once it occurs in a population, because of strong selection pressure and nonpleiotropic genetic determinants. Rothstein calculated that parasitized populations would require from 20 to 100 years to go from 80% acceptance to 80% rejection of cowbird eggs. Presumably, there must also be a period when the rejection rate is at zero before the trait makes its initial appearance in the parasitized population.

The recent contact of the Village Weaver with the Shiny Cowbird in Hispaniola argues against the possibility that this Village Weaver population has evolved egg-rejection defenses, even though selection value for such adaptation must be high. Alternatively, the egg-rejection levels may reflect the presence of intraspecific brood parasitism, although there is little evidence for its existence among weavers (Victoria, 1972; A. Cruz, pers. observ.). The low level of egg rejection presently observed in Hispaniolan Village Weavers is to be attributable to the incomplete decay of a once common adaptation rather than to recent cowbird parasitism or to intraspecific parasitism.

One may predict that, through time, the

rejection of foreign eggs will become more prevalent in Hispaniolan populations of the Village Weaver. The time framework for this chain of events is difficult to predict; the evolution of the egg-rejection trait might take considerably longer than the time predicted by Rothstein for some North American species. Any factor that decreases the rate of parasitism will decrease the selective value of the host's rejection behavior, thus slowing the increase in rejection rate. Village Weavers, for example, have an extended breeding season, and we located active colonies from March to October. By having such an extended breeding season, certain populations of the Village Weaver might escape parasitism by breeding outside the cowbird's reproductive period and, consequently might not be subject to selection favoring egg-rejection behavior. Also, selection against cowbirds brought about by egg rejection might result in a reduced incidence of parasitism in the Village Weaver and, hence, reduced selection for rejection (Rothstein, 1975a); however, Rothstein (1976) and Mason (1986a, 1986b) found that cowbirds do not strongly avoid nests of rejecter species. The recent range expansion of the Shiny Cowbird has resulted in a mosaic of parasitized and nonparasitized host populations (Wiley, 1985; Cruz et al., 1985). Thus, there is likely to be geographic variation in the frequency of rejection behavior toward cowbird eggs.

Conclusions

We have shown that on Hispaniola the Village Weaver is primarily an acceptor species and that the increase in egg-acceptance behavior may have evolved in the absence of avian brood parasitism. The recent arrival of the Shiny Cowbird on Hispaniola has allowed us to document the impact of brood parasitism on a population that has largely lost the egg-rejection behavior. Future studies on the Village Weaver on Hispaniola will examine this quantifiable selection pressure and determine its effect on the incidence of egg rejection as a host defense against brood parasitism.

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