Egg rejection behavior in a population exposed to parasitism: Village Weavers on Hispaniola

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In contrast to African Village Weavers (Ploceus cucullatus) that are parasitized by Diederik Cuckoos (Chrysococcyx caprius), introduced weavers on Hispaniola existed without parasitism for at least 2 centuries until the arrival of the Shiny Cowbird (Molothrus bonariensis) in the 1970s. Cruz and Wiley (1989) found that Hispaniolan weavers had a lower rejection rate of foreign eggs than African populations. Subsequently, Robert and Sorci (1999) and Lahti (2005, 2006) found that acceptance of dissimilar eggs is not characteristic of the species throughout its Hispaniolan range. In 1999–2002, we studied egg rejection in Hispaniolan weavers on a broad regional scale. Rejection increased as experimental eggs became increasingly different from the host eggs. Rejection rates for mimetic eggs, different color eggs, different-spotted eggs, and cowbird eggs was 23.2%, 33.3%, 61.5%, and 83.5%, respectively, with higher rejection of cowbird eggs in areas where cowbirds were observed. Although rejection is likely to have a genetic component, the differences could be due to phenotypic plasticity. Plasticity in egg rejection may be expected, given the potential cost of rejection and the spatiotemporal distribution of cowbirds. Thus, egg rejection has not necessarily decreased in Hispaniolan weavers, but it may act in a plastic manner, increasing where cowbirds are present. Key words: egg rejection behavior, Hispaniola, Molothrus bonariensis, Ploceus cucullatus, Shiny Cowbird, Village Weaver. [Behav Ecol 19:398–403 (2008)]

Recognition and rejection of foreign eggs is an adaptive behavior used by many avian taxa exposed to the selective pressure of brood parasitism (Rothstein 1982; Davies and Brooke 1989a; Ortega 1998; Martin-Vivaldi et al. 2002; Peer et al. 2005). A case in point involves the Village Weaver (Ploceus cucullatus), a polygynous, colonial-nesting species endemic to the sub-Saharan region of Africa (Collias NE and Collias EC 1970, 1971). The eggs laid by this species are among the most variable in color and pattern of any passerine species, but egg variation is low for eggs laid by individual females (Victoria 1972; Collias 1984, 1993; Cruz and Wiley 1989; Lahti 2005). The high variation between individuals coupled with the low variation within an individual female provide an egg “signature,” assuring a female weaver a high probability that the eggs within a clutch are her own (Victoria 1972; Cruz and Wiley 1989; Lahti DC and Lahti AR 2002; Lahti 2005, 2006).

African Village Weaver nests are parasitized by the Diederik Cuckoo (Chrysococcyx caprius), a species that lays eggs that show a range of spotting and color mimicking as that of weaver eggs (Victoria 1972; Fry et al. 1988; Payne 2005). African weavers reject eggs with increasing frequency as they become increasingly different in color and spotting pattern from their own eggs (Reed 1968; Victoria 1972; Collias 1984; Lahti DC and Lahti AR 2002). Victoria (1972) and Collias (1984, 1993) postulated that weavers evolved egg rejection behavior in response to cuckoo parasitism.

The Village Weaver was introduced into Hispaniola from West Africa as early as the 18th century (de Saint Mery 1797; Wetmore and Swales 1931), and it is now common in lowland and disturbed areas of Haiti and the Dominican Republic (Cruz A, personal observation). On Hispaniola, the Village Weaver existed without the selective pressure of brood parasitism for at least 2 centuries until the arrival of the Shiny Cowbird (Molothrus bonariensis). The cowbird was originally confined to South America, Trinidad, and Tobago. However, in the last 100 years it has spread throughout the West Indies (Cruz et al. 1989, 1998). Cowbirds were first observed in Hispaniola in 1972 (Post and Wiley 1976), and by the 1980s, cowbirds had become established in many lowland areas and were using weavers as hosts (Arendt and Vargas Mora 1984; Cruz and Wiley 1989).

In a study conducted in 1982, Cruz and Wiley (1989) found that weaver populations in southern Dominican Republic had a lower rate of rejection of experimental eggs than African populations. For Village Weavers laying plain eggs, the rejection rates of plain and spotted weaver eggs were 15.0% and 13.3%, respectively, and of cowbird eggs, 16.7%. Similarly, for weavers laying spotted eggs, the rejection rates of plain and spotted eggs were 18.2% and 10.0%, respectively, and of cowbird eggs, 11.8%. In contrast, Victoria (1972) found that for African Village Weavers laying plain eggs, the rejection rates of experimental plain and spotted weaver eggs were 45.5% and 73.1%, respectively. Similarly, for weavers laying spotted eggs, the rejection rates of plain and spotted eggs were 57.9% and 25.3%, respectively.

Subsequent work by Robert and Sorci (1999) and Lahti (2005, 2006) demonstrated that acceptance of dissimilar eggs is not characteristic of the species throughout its Hispaniolan range. In eastern Dominican Republic, Robert and Sorci (1999) found a high rejection rate of cowbird eggs (89.3%), moderate levels of rejection of nonmimetic weaver eggs (67.5%), and low levels of rejection of mimetic weaver eggs (25%). Robert and Sorci (1999) suggested that egg rejection behavior had increased in Hispaniolan Village Weavers. Robert and Sorci, however, relied on artificial eggs, which could have biased results (Moksnes et al. 1991; Martin-Vivaldi et al. 2002; Prather et al. 2007). Lahti (2006), using real eggs, also found high levels of egg rejection of nonmimetic weaver eggs.
and low levels of rejection of mimetic weaver eggs in north-western Dominican Republic. Lahti, however, did not examine for cowbird egg rejection. Lahti (2005, 2006) felt that there has been no significant decline in the Village Weaver’s ability to recognize foreign eggs in the introduced Hispaniolan population but that egg rejection behavior had been compromised by decreased population variation in egg appearance and increased within clutch variability, resulting in a decline in visual signature information. However, the higher acceptance of nonmimetic weaver and cowbird eggs combined with actual cowbird parasitism found by Cruz and Wiley (1989) suggests that variability exists in egg rejection among weaver populations in Hispaniola.

Because we are unable to know rejection rates in the original introduced weaver population, we do not know whether the reduction observed by Cruz and Wiley (1989) was as a result of a cost associated with egg rejection. Such costs include recognition errors, in which one’s own is mistaken for a parasitic egg and rejected (Davies and Brooke 1988, 1989b; Marchetti 1992; Lotem et al. 1995), and ejection costs, in which the host could damage its own eggs while trying to eject the parasitic egg (Marchetti 1992; Raskáfi et al. 1993). Models suggest that even a low rate of making errors in rejection of a parasitic egg can favor acceptance of such an egg if parasitism is sufficiently rare (Davies and Brooke 1989b; Davies et al. 1996). A species that evolves rejection behavior 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 1975b). This near neutrality may 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 (Rothstein 1975b; Cruz and Wiley 1989).

From 1999 to 2002, we undertook an intensive study of egg rejection behavior of Village Weaver populations in the north-western, central, and southwestern regions of the Dominican Republic. Our goals were to document the level of egg rejection by weavers on a broader regional scale. We were interested in determining if there were between-population differences in patterns of egg rejection. Differences in egg rejection by Hispaniolan weavers were to be expected, given the potential cost of rejection and the distribution in space and time of cowbirds in Hispaniola (Arendt and Vargas Mora 1984; Prather et al. 2007). We predicted that weavers would accept mimetic weaver eggs but would reject nonmimetic weaver and cowbird eggs but that there would be interpopulation differences in levels of rejection, with higher levels of cowbird egg rejection in areas, where cowbirds were present.

**METHODS**

**Study area**

We experimentally parasitized weaver nests at 7 colonies in the central part of the Dominican Republic (Bonao and San Francisco de Macorís), 11 colonies in the northwest (Monte Cristi and Luperon), and 9 colonies in the southwest (Pedernales and Jimani). Weaver colonies were typically in large trees in cattle pastures and around the edges of agricultural fields, especially rice. Number of nests experimentally parasitized within a colony ranged from 9 to 107, and we typically parasitized nests within a colony over a 3- to 4-week period during a single year. Because we did not mark birds, we could not be absolutely certain that we did not parasitize multiple nests of the same female. Nevertheless, we feel that because we parasitized nests in a large number of scattered colonies and did not visit the colonies for long periods, pseudoreplication was minimized in our experiments.

**Methods**

We used real weaver eggs taken from active nests to experimentally parasitize other weaver nests. As real cowbird eggs were not readily available to us, we also used weaver eggs that were painted with white acrylic paint, spotted, and glazed to look like cowbird eggs. Shiny Cowbird eggs are similar in size to Village Weaver eggs, although they tend to be a little shorter and wider. Weaver eggs ranged from 14.2 to 16.8 mm in width (mean 15.5 ± 0.6 mm standard deviation) and from 19.8 to 26.5 mm in length (mean 23.1 ± 1.1 mm). Real Shiny Cowbird eggs averaged 16.5 ± 0.6 mm in width and 20.7 ± 0.9 mm in length (Cruz and Wiley 1989). Similarly, egg masses were within the range of variation exhibited by real weaver and cowbird eggs. Mass of real weaver eggs ranged from 1.7 to 3.4 g (mean 2.6 ± 0.5 g, Din 1992) and that of cowbird eggs ranged from 2.5 to 3.5 g (mean 3.0 ± 0.32 g, Manolis 1982). Lahti DC and Lahti AR (2002) found that African Village Weavers did not use egg size or shape to recognize foreign eggs in their nests. In addition, if egg size and shape were important, then the use of weaver-sized eggs instead of cowbird-sized eggs should result in a lower rate of rejection.

We used 4 classes of experimental eggs: 1) “mimetic”—eggs that closely resembled the real eggs in a nest in both ground color and spotting pattern; 2) “different ground color”—eggs that were similar in spotting to the real eggs but differed in ground color; 3) “different spotting”—eggs that were similar in ground color to the real eggs but were either spotted or unspotted to differentiate them from the real eggs; and 4) “cowbird”—eggs that were painted to resemble cowbird eggs, henceforth cowbird eggs. Cowbird eggs were the most divergent in appearance. We also used some nests as “control” nests; these cases, the eggs were manipulated in the same way as eggs from experimental nests, but all the original eggs were returned to the nest and no foreign eggs were added. In the northwestern and central Dominican Republic, the choice of foreign eggs for each trial was determined using randomly generated tables with the following percentages: 30% mimetic, 20% different color, 20% different spotting, 20% cowbird, and 10% control. In the southwest, only the mimetic, cowbird, and control egg types were used with approximately the following percentages: 70% mimetic, 20% cowbird, and 10% control.

We visited active weaver colonies every 2-6 days. Nests could have been checked more often because egg rejection by Village Weavers normally occurs within 24 h of parasitism (Victoria 1972; Cruz A, personal observation). We used longer periods between checks, however, to minimize disturbance at the colonies. On each visit to a colony, we checked all nests that were accessible from the ground or from ladders placed against the colony tree. We determined nest contents by reaching through the entrance hole and gently feeling the interior. For each nest that contained eggs, we removed the eggs and recorded their number, color, and spotting pattern. We marked each nest using a small numbered piece of tape placed on a twig adjacent to the nest. In nests that contained only 1 egg, the egg was returned to the nest and a foreign egg was also added. In nests that contained more than one egg, one of the eggs was removed for use in other parasitism experiments and the remaining eggs were returned to the nest along with a foreign egg. Eggs used in experimental parasitism were marked with a small dot on the wide end of the long axis using an indelible ink marker so that they could be differentiated from other eggs in the nest. In control nests, the eggs were removed and I was marked as described above. All eggs were then returned to the nest. On return trips to the same colony, new nests with eggs were experimentally parasitized...
and previously parasitized nests were checked and their contents recorded.

In some cases, mainly in nests that we parasitized on our first visit to a new colony, the eggs hatched before we were able to return for our second check, and we discarded those nests from analysis. In addition, we did not include data from any nest for which we could not find the marker tape. Our experimental parasitism took place in the egg-laying or early incubation stages of the nesting cycle, and we only parasitized new nests within each colony on subsequent visits. Foreign eggs were considered “accepted” if they remained in the nest and were not embedded in the lining of the nest and “rejected” if they were missing from the nest or embedded in the lining of the nest. Some nests ended up completely empty, either due to predation or abandonment, and these were recorded in a separate category.

### Analyses

By visiting the colonies regularly, we minimized the number of nests that would have been parasitized late in the incubation stage. Nevertheless, egg rejection rates have been shown to differ for some species between stages of the nesting cycle (Rothstein 1975a; Lawes and Kirkman 1996; Welbergen et al. 2001). To test for differences in egg rejection rates for nests that were parasitized in the egg-laying versus incubation stages, we performed a 2 × 2 chi-squared test on the 70 nests that we parasitized with mimetic eggs and that did not end up empty. We used chi-squared likelihood-ratio tests (Table 1) to test whether the possibility of a nest ending up empty was independent of the region in which the experiment took place. A single test was done for each of the 5 types of egg used (control, mimetic, different spotting, different color, and cowbird) across all regions. In addition, we used a chi-squared likelihood-ratio test to determine if the proportion of nests ending up empty differed across regions when all egg types were lumped together (Table 2).

For the remaining tests, we eliminated empty nests and control nests from consideration in the analysis (see Results). We used chi-squared likelihood-ratio tests to determine if there were significant between-site differences in the rejection rates of a given egg type (Table 2). We did not test experiments using control eggs because no control eggs were rejected at any site, making a test unnecessary. Thus, there were a total of 4 tests, 1 each for mimetic, different-spotting, different color, and cowbird egg types.

As a final set of tests, we used chi-squared likelihood-ratio tests to determine whether significant differences existed in the rejection rates of different egg types (mimetic, different spotting, different color, and cowbird) within each of the 3 regions (Table 3). First, we did a global chi-squared likelihood-ratio test to determine if there were between-type differences in rejection rates across all egg types. If these results indicated significant differences, we then used chi-squared likelihood-ratio tests to look for differences in rejection rates between individual egg types. These tests were performed along a gradient of increasing differentiation from the eggs in the nests. For experiments from the northwest and central regions, we tested mimetic versus different color, different color versus different-spotting, and different-spotting versus cowbird egg types (Table 3). In the southwest, where only the mimetic and cowbird egg types were used, we tested for differences in rejection rates between those 2 types (Table 3).

### RESULTS

We found no significant differences (degrees of freedom [df] = 1, $\chi^2 = 0.37, P = 0.54$) in the egg rejection rates between nests that were parasitized with mimetic eggs during the egg-laying stage (5 of 12, 25%) and those that were parasitized with mimetic eggs during incubation (10 of 58, 17.2%). Thus, for further tests, we assumed that egg rejection rates were independent of the stage in which the nest was parasitized.

The percentage of nests that ended up empty during our egg rejection experiments ranged from 3.4% (eggs with different spotting in the northwest) to 18.5% (cowbird eggs in the central region) with a mean of 8.7%. We did not find any significant among-site differences in the percentage of nests that ended up empty (Table 1). When all sites were considered together, the chance of a nest ending up empty was independent of the type of egg used in the experiment (df = 4, $\chi^2 = 2.13, P = 0.71$). Thus, the probability of a nest ending up empty was not
Results of chi-squared likelihood-ratio tests when all egg types were considered in the same test.

<table>
<thead>
<tr>
<th>Egg type</th>
<th>Percentage of eggs rejected by location</th>
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<tbody>
<tr>
<td></td>
<td>Northwest</td>
</tr>
<tr>
<td>Mimetic (A)</td>
<td>21.2</td>
</tr>
<tr>
<td>Different color (B)</td>
<td>21.4</td>
</tr>
<tr>
<td>Different spotting (C)</td>
<td>65.5</td>
</tr>
<tr>
<td>Cowbird (D)</td>
<td>90.0</td>
</tr>
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Significant differences:
- A < B indicates that rejection rates of mimetic eggs were significantly lower than rejection rates of eggs with different spotting or different color, but the latter 2 types did not differ from each other.
- AB < CD indicates that rejection rates of mimetic eggs were significantly lower than rejection rates of eggs with different spotting or different color, but the latter 2 types did not differ from each other.

Global chi square: 34.89, 42.26, 18.49

P value: <0.0001, <0.0001, 0.0001

Influenced by our experimental design, and we eliminated empty nests from consideration in further testing.

For control nests, we did not find any evidence that egg rejection occurred (Table 2). Thus, we assume that egg rejection did not take place due to manipulation of the eggs. We did not find any significant among-site differences in egg rejection rates for any of the other egg types (Table 2). However, variability in egg rejection existed among sites. Different ground color eggs were rejected at a higher frequency (42%) in the central region than in the northwest (21%). Similarly, there were nearly significant (P = 0.07) among-site differences in the rejection rates of cowbird eggs. Thus, we performed post hoc tests to determine whether egg rejection differed between pairs of sites. There were trends toward significant differences in rejection rates between the northwestern and southwestern sites (df = 1, χ² = 2.73, P = 0.10) and between the central and southwestern sites (df = 1, χ² = 4.74, P = 0.03). There were no significant differences between rejection rates in the central and northwestern sites (df = 1, χ² = 0.07, P = 0.79). When results from the northwestern and central sites were combined, there were significant differences in the rejection rates of cowbird eggs between these sites and the southwestern site (df = 1, χ² = 4.04, and P = 0.04).

We found significant differences in the rejection rates of experimental eggs types in each of our sites (Table 3). In general, rejection rates increased as the experimental egg became increasingly different from the eggs in the nest. On average, mimetic eggs were only rejected 23.2% of the time (39 of 168), different ground color eggs were rejected 33.3% (11 of 33) of the time, different-spotting eggs were rejected 61.5% (32 of 52) of the time, and cowbird eggs were rejected 85.3% (58 of 68) of the time.

DISCUSSION

Timing of parasitism, host response, and empty nests

Interpretation of the results of egg rejection experiments can be biased in several ways, and we attempted to control for as many variables as possible. Previous studies have shown, for example, that the timing of the parasitism event can influence rejection rates in some species (Rothstein 1975a; Lawes and Kirkman 1996; Welbergen et al. 2001; but see Lotem et al. 1995). In most cases, we were able to parasitize nests in the egg-laying or very early incubation stages, and our data using mimetic eggs suggest that rejection rates did not differ between these stages. We did not use any data from a nest in which young hatched before we returned for our check.

Experimental results could also be biased by incorrect interpretation of empty nests. Nests may end up empty due to many factors including egg rejection, predation (Martin 1992), or abandonment of the nest either due to disturbance or egg breakage during manipulation (Salathe 1987). However, our results suggest that the probability of a nest ending up empty was roughly similar across all sites and among all egg types (Table 1). We believe that our 9% mean of nests ending up empty reflects a “background rate” of nest failure. In our study, these nests may either have been depredated or abandoned, but our results suggest that the exclusion of empty nest data from our analyses of rejection rates did not influence our results. The high rate at which nests parasitized with cowbird eggs ended up empty in our central study site (18.5%) suggests that egg type may have influenced the results. However, the rates at which nests parasitized with cowbird eggs ended up empty at other sites were at or below average and, in the northwest, both control nests and nests parasitized with mimetic eggs also ended up empty at higher than expected rates (14.3% and 13.2%, respectively). We also found no evidence to suggest that there was any rejection of eggs in control nests (Table 2), indicating that manipulation of the eggs did not affect our results.

General patterns of egg rejection

Our results show that Village Weavers on Hispaniola reject foreign eggs in their nests with increasing frequency as these eggs become increasingly different, either in color or spotting pattern, from those in the nest (Table 3). These results follow expected patterns based on rejection experiments on African weaver populations (Victoria 1972; Collias 1984; Lahti DC and Lahti AR 2002), where weavers are parasitized by the Diederik Cuckoo. The percentages of eggs rejected by weavers in our study are similar to those obtained for African weavers by Lahti DC and Lahti AR (2002). For example, using logistic regression, they suggest that mimetic eggs would be rejected about 20% of the time, which is similar to our results (Tables 2 and 3). Also, rejection values for eggs with different-spotting and different color patterns (Table 2) were within the range found in their study although the Hispaniolan population had a lower level of variation between individuals in egg color and spotting than did the African (Gambian) population (Lahti 2005).

Our results are consistent with results obtained by Robert and Sorci (1999). In 1998, using plaster eggs to parasitize weaver nests in the Eastern Dominican Republic, Robert and Sorci found a 67.5% rejection rate of nonmimetic eggs (40 nests) and a 25% rejection rate of mimetic eggs (16 nests), as compared with a 60% rejection rate of nonmimetic eggs and 19% rejection rate of mimetic eggs in our study (Table 2). Robert and Sorci (1999), however, included data from only 56 nests from a small area of Hispaniola and relied on artificial eggs, which could have biased results (Moksnes et al. 1991; Martin-Vivaldi et al. 2002; Prather et al. 2007). Similarly, Lahti (2006), using real weaver eggs to parasitize weavers’ nests in the northeastern Dominican Republic, found a 64.3% rejection of nonmimetic eggs. Lahti’s study covered 1 breeding season with a sample size of 62 nests (Lahti 2006). We were able to expand on their results, covering a larger geographical area more than 3 field seasons (March through September) and using larger sample sizes of real weaver eggs (n = 275) and cowbird eggs (n = 68).
Rejection of cowbird eggs

Our results on cowbird egg rejection by Hispaniolan weavers agree with those of Robert and Sorci (1999), who found an 89% rejection rate of artificial cowbird eggs (15 nests) as compared with an average rejection rate of 85% (68 nests) for our 3 sites. However, in southwestern Dominican Republic, weavers reject cowbird eggs at a lower rate (73%) than in the northwest (90%) and central regions (96%) (Table 2). The southwest was colonized by cowbirds later than the central and northwestern areas (Arendt and Vargas Mora 1984), and we rarely saw cowbirds, suggesting that this population may have had fewer interactions with cowbirds.

In contrast, cowbirds were more common in the central and northwestern region (Luponero), where we saw flocks numbering more than 100 individuals and in many instances feeding with weavers. Cowbirds were in the vicinity of weaver colonies, and on several occasions in the central region, we saw cowbirds entering colonies and inspecting weaver nests. We did not, however, find parasitized nests. The absence of cowbird eggs in weaver nests is most likely related to the high rejection rate (Table 2) recorded in these colonies. Additionally, the higher percentage (18.5%) of nests with experimental cowbird eggs that ended up empty in our central study site may be related with the increased presence of cowbirds in this region.

Possible reasons for variation in egg rejection behavior

Cruz and Wiley (1989) found that parasitism by the Shiny Cowbird had a detrimental impact on the Village Weaver by reducing productivity, and parasitized nests fledged 0.67 weavers per nest and unparasitized nests fledged 2.0 weavers per nest. Selection might favor those individuals that are able to recognize their eggs and reject dissimilar eggs. Robert and Sorci (1999) showed that, theoretically, the increased rate of rejection of foreign eggs could be related to an evolutionary response of the weavers to the selective pressure of cowbird parasitism.

However, the relatively recent contact of the Village Weaver with the Shiny Cowbird in Hispaniola also suggests an alternative explanation to an evolutionary response, even though selection value for such adaptation might be high. Cowbird eggs are nonmimetic and differ in color (off-white) and spotting pattern (typically having larger spots and more even spotting) from weaver eggs. Thus, weavers should be able to distinguish and reject these distinct eggs at a high rate. If the increase in egg rejection behavior in weavers was an evolutionary response to cowbird parasitism, we would expect to see high rejection rates of cowbird eggs and relatively low rejection rates of weaver eggs regardless of differences between the foreign weaver eggs and the host eggs. Instead, our data suggest that we are seeing a pattern of rejection similar to that seen in African populations of Village Weavers, where it is advantageous to be able to distinguish all foreign eggs due to the mimetic properties of the Diederick Cuckoo eggs.

In experiments with Brown-headed Cowbird (*Molothrus ater*) hosts, Rothstein (1982) found that rejection is not specific to cowbird eggs. Rothstein suggested that birds have apparently responded evolutionarily to brood parasitism by developing recognition of their own eggs and intolerance to divergent eggs rather than by developing recognition and rejection specific to parasitic eggs.

Experiments suggest that the mechanism of egg recognition in passerines is based on an imprinting-like process (Victoria 1972; Rothstein 1974, 1978; Lotem et al. 1995; Rodriguez-Gironés and Lotem 1999), where naive hosts learn to recognize as their own egg types, the eggs they see in their nests. As a female lays more and more clutches, this process could allow her to fine-tune her choice and only accept eggs similar to the ones she has laid in the past and reject different egg types. Lahti DC and Lahti’s AR (2002) study suggests that West African Village Weavers have a “remarkably precise memory for the colour and spotting pattern of their own eggs.”

Although egg rejection is likely to have a genetic component (Rothstein 1975a), the differences observed in egg rejection rates among populations could be a result of phenotypic plasticity (Brooke et al. 1998; Lindholm 2000). We suggest that the differences in egg rejection behavior we observed may be the result of behavioral changes in egg rejection resulting from parasitism by cowbirds. This view is supported by the higher rejection of cowbird eggs that we found in the central and northern regions, an area where cowbirds were frequently observed. Furthermore, in the population (Santo Domingo, southern Dominican Republic) that Cruz and Wiley (1989) recorded low rejections of nonmimetic and cowbird eggs (14.5%, n = 110), cowbirds were not recorded in the area. Thus, egg rejection has not necessarily decreased in Hispaniolan weavers (Lahti 2005, 2006), but it may act in a plastic manner, increasing in frequency in areas were cowbirds are present. However, even in cases where phenotypic plasticity exists, genetic variation may be present and response to the selective pressure of brood parasitism (Brooke et al. 1998; Lindholm 2000).

In Reed Warblers (*Acrocephalus scirpaceus*), evidence suggests that phenotypic plasticity can explain the observed differences in egg rejection behavior by different populations in Europe (Brooke et al. 1998; Lindholm 2000). As noted by Lindholm (1999), the potential of a host being parasitized varies across a spatiotemporal scale, “suggesting that it could be advantageous for hosts to modulate anti-parasite behavior accordingly.” Thus, in Village Weavers, as in Reed Warblers, the variation found in experimental egg rejection may be the consequence of phenotypic plasticity with shifts in the balance of costs and benefits of rejecting eggs under different conditions (Davies and Brooke 1988, 1989b; Lotem et al. 1995; Brooke et al. 1998; Lindholm 2000; Lindholm and Thomas 2000). Our results and the results of the earlier study (Cruz and Wiley 1989) suggest that different Hispaniolan Weavers populations (as noted in the case of Reed Warblers) may not differ in their ability to recognize a foreign egg in the nest but that they differ primarily in their reaction, being more tolerant of the foreign egg when the frequency of parasitism is lower or costs of egg rejections are lower (Lindholm 2000).

Mechanisms by which egg rejection is maintained in population

One hypothesis is that weavers maintain a very low level of egg rejection due to intraspecific brood parasitism. Although intraspecific parasitism is common in the Masked Weaver (*Ploceus taeniopyerus*) (Jackson 1998), a sister species to the Village Weaver, it apparently occurs at very low rates in Village Weaver populations in Africa (Victoria 1972; Collias 1984; Lahti DC and Lahti AR 2002). We found only 2 definite cases of intraspecific parasitism, although we note that rejection rates of nonmimetic eggs are high, which would mean that actual detection rate of intraspecific parasitism would be much lower than the actual rate.

Under these circumstances it would be reasonable to assume that egg rejection rates would be different for mimetic and nonmimetic eggs. If, on the other hand, the ability to recognize foreign eggs is a response that functions as a plastic behavior that is facultatively expressed rather than deterministic (Lotem et al. 1995; Davies et al. 1996; Lindholm and Thomas 2000), then we would expect egg rejection to decrease, when
parasitism is low or not present, and increase as levels of parasitism increase (Brooke et al. 1998). Thus, we would expect rejection to vary across time and space.

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