

PERSISTENCE OF EGG RECOGNITION IN THE ABSENCE OF CUCKOO BROOD PARASITISM: PATTERN AND MECHANISM

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Abstract.—Broad ecological shifts can render previously adaptive traits nonfunctional. It is an open question as to how and how quickly nonfunctional traits decay once the selective pressures that favored them are removed. The village weaverbird (*Ploceus cucullatus*) avoids brood parasitism by rejecting foreign eggs. African populations have evolved high levels of within-clutch uniformity as well as individual distinctiveness in egg color and spotting, a combination that facilitates identification of foreign eggs. In a companion study, I showed that these adaptations in egg appearance declined following introductions of weavers into habitats devoid of egg-mimicking brood parasites. Here, I use experimental parasitism in two ancestral and two introduced populations to test for changes in egg rejection behavior while controlling for changes in egg appearance. Introduced populations reject foreign eggs less frequently, but the ability of source and introduced populations to reject foreign eggs does not differ after controlling for the evolution of egg color and spotting. Therefore, egg rejection behavior in introduced populations of the village weaver has been compromised by changes in egg appearance, but there has been no significant decline in the birds' ability to recognize foreign eggs. This result reconciles earlier studies on this system and provides insights into the ways behavior can change over generations, especially in the context of recognition systems and the avoidance of brood parasitism.

Key words.—Adaptation, brood parasitism, diderik cuckoo, egg rejection, introduced species, Ploceidae, reverse evolution, trait loss, village weaver.

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Darwin (1859, ch. 15) argued that “use and disuse” should impose a “considerable effect” on the evolution of traits maintained by natural selection. A principal prediction is that adaptive traits will decay if changes in the selective environment lead to a loss of functionality. Empirical studies have since shown that the rate of decay of apparently nonfunctional traits varies, for reasons that are not always obvious. Some lose integrity quickly (Fong et al. 1995; Eckert et al. 1999), whereas others persist intact as relicts for hundreds or thousands of generations (Coss 1999; Rothstein 2001). Explaining why a behavioral trait persists or decays can be especially challenging, for at least two reasons. First, a nonfunctional trait should decline rapidly if it is costly. Given that behavior is often conditional in its expression, however, the cost of a nonfunctional behavior may be low; if not expressed, it may not be subject to selection. Second, behavior is always part of a suite of traits, a complex coexpressed character set (West-Eberhard 1989; see also Alexander 1990), that includes features of the nervous and endocrine systems as well as morphology involved in the execution of the behavior. Thus, an observed decay in the expression of a behavior may result from a variety of mechanisms. Here I report an instance of short-term decay in a behavioral trait and demonstrate experimentally the major mechanism for the change.

Some birds have the ability to identify and discard eggs laid by brood parasites (Swynnerton 1918; Payne 1977). Several studies have documented change in egg rejection behavior in a host species, by either gathering longitudinal data or comparing two populations that differ in brood parasitism (e.g., Davies and Brooke 1989a; Briskie et al. 1992; Brooke et al. 1998; Lindholm and Thomas 2000). For instance, re-

jection of nonmimetic eggs in a population of reed warblers (*Acrocephalus scirpaceus*) declined precipitously over a 12-year period during which the rate of common cuckoo (*Cuculus canorus*) parasitism declined (Brooke et al. 1998). The mechanisms for such changes in the tendency to reject foreign eggs are poorly known (Payne 1997; Brooke et al. 1998; Lindholm and Thomas 2000; Rothstein 2001). Rejection of foreign eggs is the behavioral component of a suite of maternal traits including, among other things, egg appearance and a visual recognition system (Beecher 1991; Mateo 2004). A change in either egg appearance or recognition may by itself result in a change in the frequency of egg rejection behavior. When a brood parasite mimics the eggs of its host (Payne 1967; Davies and Brooke 1989b), host egg appearance may evolve to counter this mimicry (Stokke et al. 2002b; Lahti 2005). In particular, rejection of foreign eggs is facilitated by uniformity of eggs within a clutch (Davies and Brooke 1989b) combined with distinctiveness of eggs from those of conspecifics, and thus from parasites that track population patterns in egg appearance (Baker 1913).

The village weaverbird (*Ploceus cucullatus*) is subject to brood parasitism by the egg-mimicking diderik cuckoo (*Chrysococcyx caprius*) in its ancestral range in sub-Saharan Africa. Village weavers in Africa lay eggs that are consistent in appearance (color and spotting) within a clutch, yet variable among individuals; they use this signature information to identify and reject foreign eggs (Victoria 1972; Collias 1984; Lahti and Lahti 2002). The village weaver has been introduced twice independently to islands without cuckoos, Hispaniola and Mauritius (Fig. 1). In these populations, variation in egg appearance is high within clutches and low between individuals relative to their source populations in Africa (Lahti 2005; see Fig. 2). This indicates that selection from cuckoo parasitism maintains individual distinctiveness and clutch consistency in Africa and that these adaptations

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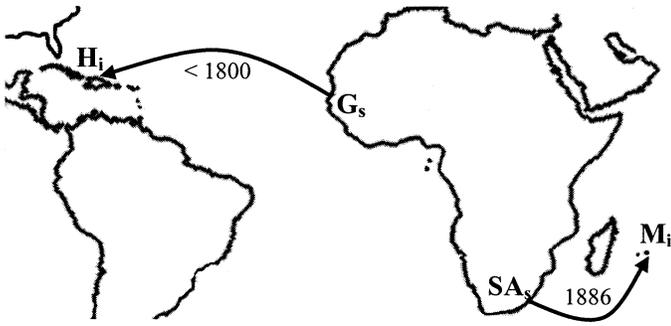


FIG. 1. Populations of the village weaver (*Ploceus cucullatus*) examined in this study. The two African populations (G_s , The Gambia; SA_s , South Africa) are within the natural range, in sympatry with the brood parasitic diederik cuckoo (*Chrysococcyx caprius*); the two island populations (H_i , Dominican Republic; M_i , Mauritius) have been introduced and are not sympatric with any egg-mimicking brood parasite.

have decayed on Hispaniola and Mauritius following release from parasitism. Previous work on this and other bird species suggests that the observed changes in egg color and spotting were evolutionary rather than environmentally induced (Punnett and Bailey 1920; Punnett 1933; Goodman and Shealy 1977; Collias 1984; 1993; Mikšík et al. 1996; Hunt et al. 1999).

Another question is whether the tendency to reject eggs has also decayed in the introduced populations. A lower frequency of egg rejection may be an inevitable consequence of the changes in egg appearance in both introduced populations. The increase in within-clutch variation would increase the range of egg appearance over which a foreign egg effectively mimics a given host clutch. Similarly, the decrease in population variation would increase the likelihood that a brood parasite whose eggs have been tracking the host population (or conspecific eggs, a proxy) would match the eggs of a given host individual. Assuming some change in egg rejection, three hypotheses address possible mechanisms: H_1 , change of egg rejection behavior in the introduced weavers is solely a by-product of the evolution of egg appearance; H_2 , the egg recognition system (e.g., a perceptual or cognitive trait) has evolved in the introduced weavers, contributing to a loss of precision in egg recognition and a lower frequency of egg rejection behavior; and H_3 , a plastic change in rejection behavior in the introduced weavers is induced by the absence of an environmental cue associated with brood parasitism, such as perception of adult cuckoos (e.g., Davies et al. 1996).

I compare egg rejection behavior of the village weaver in South Africa, within the ancestral range where birds are parasitized by the diederik cuckoo, with rejection behavior on Mauritius, an island without egg-mimicking brood parasites and where the village weaver was introduced from Southern Africa in 1886 and is now abundant (Lever 1987; Lahti 2003). I also compare rejection behavior in The Gambia, a parasitized source population in West Africa, with that on Hispaniola, a Caribbean island without egg-mimicking brood parasites and where the village weaver was introduced from West Africa more than two centuries ago and is now abundant (Lever 1987; Lahti 2003). Assuming a generation time of about 1.9 years (based on an approximate mortality rate of

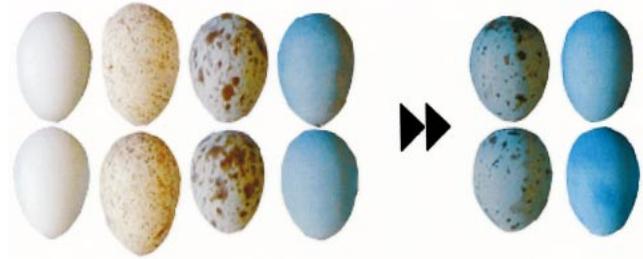


FIG. 2. Examples of village weaver eggs from two study sites: The Gambia (left), from which village weavers were introduced more than 200 years ago to Hispaniola (right). The pair of eggs in each column come from the same clutch. Population variation in color and spotting has decreased following introduction, and within-clutch variation has increased.

0.5 per year), the introduced populations have diverged from their sources for about 60 generations (Mauritius) and more than 100 generations (Hispaniola). In these introduced populations, within-clutch variation in egg color and spotting has increased and between-individual variation has decreased (Lahti 2005). The methods I employ here attempt to isolate the portion of behavioral change that might be attributable to recognition system evolution or to behavioral plasticity, rather than evolution of egg appearance. I experimentally parasitized nests in all four populations while controlling for differences in egg appearance between populations.

Two previous studies tested the responses of Hispaniolan village weaver females to experimental parasitism. Cruz and Wiley (1989) measured egg rejection behavior in Hispaniola between 1974 and 1982 and concluded that rejection was less frequent than the presumed African level based on the results of Victoria (1972). Cruz and Wiley (1989) therefore classified the village weaver on Hispaniola as an “accepter” population. In contrast, results of experiments by Robert and Sorci (1999) showed a high frequency of egg rejection, similar to that in the captive population studied by Victoria (1972). Robert and Sorci (1999) interpreted the difference between their results and those of Cruz and Wiley (1989) as indicating a rapid increase in rejection behavior (i.e., a reversion to high discriminatory abilities) during the 16 years between the two studies as a result of evolutionary or perhaps plastic changes favored by newly established sympatry with an expanding population of brood parasitic (but not egg-mimetic) shiny cowbirds (*Molothrus bonariensis*).

Methodological differences between studies allow for alternative explanations for the results of Cruz and Wiley (1989; see Payne 1997, 1998; Brooke et al. 1998; Rothstein 2001) and therefore raise questions about Robert and Sorci’s (1999) interpretation of short-term change between 1982 and 1998. Although the time-sensitive nature of tests of rapid evolution in natural systems makes true replication of these studies impossible, I approximated the methods of Cruz and Wiley (1989) and Robert and Sorci (1999) to test the extent to which their results indicate changes in rejection behavior (Rothstein and Robinson 1998; Underwood and Sealy 2002), as opposed to particulars of methodology (Payne 1997; Rothstein 2001).

I also report the frequency of an incidental cost of rejection,

which occurs when hosts eject their own eggs in the process of removing foreign eggs (Stokke et al. 2002a).

MATERIALS AND METHODS

Experimental Parasitism

I replaced village weaver eggs with conspecific eggs to mimic parasitism by conspecifics or the diederik cuckoo, as in Lahti and Lahti (2002; see also Rothstein 1975). The data in Lahti and Lahti (2002) are included in this analysis; those data were gathered on Janjangbureh Island, The Gambia, West Africa (13°35'N, 14°40'–50'W; July–August 1999; $N = 96$; hereafter G_s , the subscript indicating a source population). Experiments were also conducted near Pietermaritzburg, KwaZulu-Natal, South Africa (29°25'–45'S, 30°25'–35'E; October–December 2000; $N = 102$; hereafter SA_s); Black River and Rivière du Rempart Divisions, Mauritius (20°00'–20'S, 57°20'–40'E; December 2000 to February 2001; $N = 59$; hereafter M_i , the subscript indicating an introduced population); and Monte Cristi and Valverde Provinces, Dominican Republic, Hispaniola (19°35'–45'N, 71°00'–20'W; April–June 2001; $N = 137$; hereafter H_i ; Fig. 1). Lack of some measurements (particularly spectra) of some eggs decreased sample sizes for some analyses.

On the cap (broad end) of each host egg and experimental egg I wrote a number for identification. In each case I replaced one host egg with a foreign egg, as the diederik cuckoo is known to do (Friedmann 1968). In some cases the experimental egg replaced the only egg in the host nest; whether a host egg is in the nest for comparison was previously found not to affect rejection in this species (Lahti and Lahti 2002). I replaced eggs between 0800 and 1200 h. Study nests were unmarked; a numbered tag was placed more than 1 m from each nest during the experimental period. All nests were parasitized experimentally during or within 3 days after the female's laying period. Each nest was used only once.

Additional nests served as controls for researcher manipulation and background sources of nest destruction (G_s : $N = 20$; SA_s : $N = 15$; H_i : $N = 16$). All eggs in each of these nests were removed, marked, and replaced in the same nest. To distinguish acceptance from desertion at experimental nests, researchers observed a sample of females at the nest after the experimental period, and also checked whether individuals that were experimentally parasitized during their laying period completed their clutch and continued to incubate their eggs afterward. Deserted or predated nests were excluded from analysis (less than 1% of nests).

I checked each nest 48–52 h after egg replacement, with the exception of 54 Gambian nests that were checked 24–28 h after egg replacement. Comparison of egg rejection at 42 other nests in The Gambia revealed no difference in rejection between 24–28 and 48–52 h after replacement (Lahti and Lahti 2002), so the data using both experimental periods were pooled for further analysis. Eggs damaged or missing were considered rejected.

Control for Egg Variability Differences among Populations

Village weavers reject eggs according to the difference in color and spotting between foreign eggs and their own eggs

(Lahti and Lahti 2002). I compared weavers' rejection of differing conspecific eggs across populations to provide an initial indication of the change in rejection behavior between source and introduced populations. Conspecific eggs serve as proxies for those of an egg-mimicking brood parasite that has evolved to mimic the eggs of each population. However, an increase in within-clutch variation and decrease in between-individual variation in egg appearance was observed in the introduced populations (Lahti 2005). Although a perfect control was impossible, I used three methods to help correct for these differences so that birds could be tested, to the extent possible, as if egg variability were the same across populations.

First, population egg variability was low in the introduced populations, resulting in limited opportunities to test for rejection of eggs that were highly different from host eggs. To remedy this in part, I sought eggs with unusual appearance in the introduced populations and used these as the parasitic eggs in experiments. I also brought eggs from South Africa to use in experiments in Mauritius.

Second, on Hispaniola, available egg colors did not vary enough for conspecific egg replacements to cover the complete range of cues (in terms of difference in appearance between host and foreign eggs) presented to the source population in The Gambia; nor were Gambian eggs available for the experiments on Hispaniola. Reduced rejection of conspecific eggs on Hispaniola could be a by-product of the decrease in distinctiveness of eggs in that population, whereas extrapolation based on existing variation on Hispaniola may not provide an accurate estimate of rejection for more divergent eggs. Therefore, 71 of the experimental eggs used on Hispaniola were painted to match the finish of weaver eggshells in four different colors: one common among Hispaniolan eggs to serve as a control (dark blue-green, E13/8 in *Villalobos Color Atlas* [VCA, Villalobos-Dominguez and Villalobos 1947]; $N = 17$; see Fig. 3A for spectra), one rare among Hispaniolan eggs but common in Africa (light blue-green, VCA: E15/9), and two other colors common in Africa but absent from Hispaniola (very light blue-green, VCA: E17/3; and off-white, VCA: 19/0; see Fig. 3B). Eggs were matched in human-visible wavelengths only; no attempt was made to match eggs in the near-ultraviolet (near-UV) range, which is invisible to humans but visible to birds (Jacobs 1992). As a result, paint spectra dropped off to near 0% reflectance in the near-UV range, unlike eggshell spectra. The use of dark blue-green paint as a control therefore tests for the combined effect of painting the eggshell and its lack of reflectance in the near-UV. To further test for an artifact, "paint" was entered as a variable in statistical analysis, and all interactions with this variable were checked for significance whenever egg color was in the model. The above approaches allowed rejection behavior to be tested over a broader range of egg appearance differences, eliminating the need to extrapolate. Because likelihood of rejection is analyzed as a function of differences in color and spotting, a nonrandom collection of experimental eggs does not introduce bias, as it would if results were presented as an absolute rejection rate.

Third, differences between host and experimental eggs were calculated as the difference between the experimental egg and the most similar egg in the host clutch for each

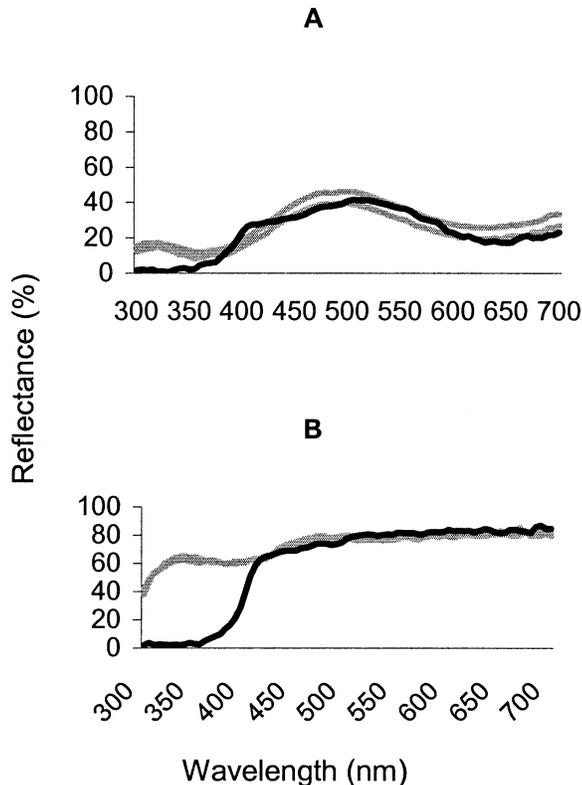


FIG. 3. Match of paint to actual village weaver egg colors (reflectance spectra): (A) dark blue-green (control); (B) off-white (experimental). Black lines are spectra of painted eggs. The two gray lines in (A) are two dark blue-green eggs from the Dominican Republic. The two gray lines in (B) are two off-white eggs from The Gambia. Wavelengths below 400 nm are in the near-UV range.

variable. When the mean egg for each variable is used, rejection behavior declines sharply in the introduced populations, as expected. In this case, some unknown proportion of the decrease is the result of the increase in egg appearance variance within a clutch. Using the egg in the host clutch that is most similar to the experimental egg yields a measure of difference in egg appearance that is less dependent on the level of variation among host eggs, although this method may not completely remove the effect of differences in clutch uniformity. For example, recognizing foreign eggs that are equally divergent from the most similar host egg may be a more difficult perceptual task when the host clutch is variable than when it is uniform.

Employing these three methods, any significant effect of population on rejection behavior would falsify H_1 by indicating a change beyond that caused by population differences in egg appearance (as proposed in H_2 and H_3).

Comparisons of Egg Appearance

Measurements were taken of mass, shape, ground color, and spotting of all host and experimental eggs. Experimental eggs were measured before each experiment, and host eggs after the experiment. Mass was measured to the nearest 0.05 g with a spring scale. I considered shape to be the ratio of length to breadth, each of which was measured with digital calipers to the nearest 0.1 mm.

A single researcher (A. R. Lahti) matched the ground color of eggs to color chips in the VCA (Villalobos-Dominguez and Villalobos 1947), as in previous studies (Lahti and Lahti 2002; Lahti 2005). However, color charts assume that color differences perceived by humans are equivalent to differences perceived by birds. In fact, birds have more and different cone types than humans, and birds can see light in near-UV wavelengths (300–400 nm; Bennett et al. 1994; Cuthill et al. 1999). Therefore, after all experiments were concluded for each population, I took the eggshells back to the United States and measured reflectance in the laboratory with an Ocean Optics USB2000 UV-VIS spectrophotometer and OOIBase32 software (Ocean Optics, Inc., Dunedin, FL). I could not locate some rejected eggs after the experiments; in these cases I used the spectral data from another egg from the clutch of the experimental egg, as long as my color chart comparison had concluded no difference in color between them; otherwise I excluded the clutch from analysis. I assessed reflectance at 5-nm intervals over the wavelength range of 300–700 nm with a 200-Hz pulsed xenon light source (Ocean Optics PX-2), and a 400- μ reflection probe (Ocean Optics R400-7) held at a 45° angle 5 mm from the sample. Integration time was set at 250-msec. I standardized measurements with a diffuse tile made of polytetrafluoroethylene that reflects more than 98% of light over all sampled wavelengths (Ocean Optics WS-1). I performed all measurements under an opaque cloth to avoid an effect of ambient light. A few eggs lacked uniformity in color, in which cases I analyzed the spectra that (based on visual inspection) characterized the largest proportion of the egg's surface area.

I summarized reflectance differences between host and experimental eggs using principal components analysis (PCA; Jolliffe 1986), which is thought to be the most appropriate means of reducing spectrophotometric data for analysis (Cuthill et al. 1999; for a similar application to this study see Jackson 1998). One PCA was performed on the data from all four populations to facilitate interpopulation comparison, although PCA based on single populations or pairs of populations produced a similar matrix of loadings. PCA reduced the variation in the data into four orthogonal principal components. PC1 explained 61.5% of the variance in the sample. It loaded consistently across the entire range of wavelengths (300–700 nm), and therefore corresponds closely to differences in brightness (Fig. 4A; see Endler 1990). PC2 explained 10.5% of the variance, and PC4 explained 3.4%; together these two components represent differences in near-UV, PC2 loading more significantly between 335 and 400 nm in wavelength and PC4 more significantly between 300 and 335 nm. The loadings of these two components presented an unexpected opportunity to test for the influence of nonredundant information in UV reflectance on egg rejection behavior. PC3 explained 3.8% of the variance and represents chroma and hue, mainly the intensity of blue-greenness (Fig. 4B). All analyses of color were performed twice, once with color chart data and once with spectral data. All results were similar. The significant variables did not differ in the two analyses, but results from color chart data were more significant, even if some data are excluded to match the spectral sample size. Only results from spectral data are presented here.

Four aspects of eggshell spotting were assessed: size, den-

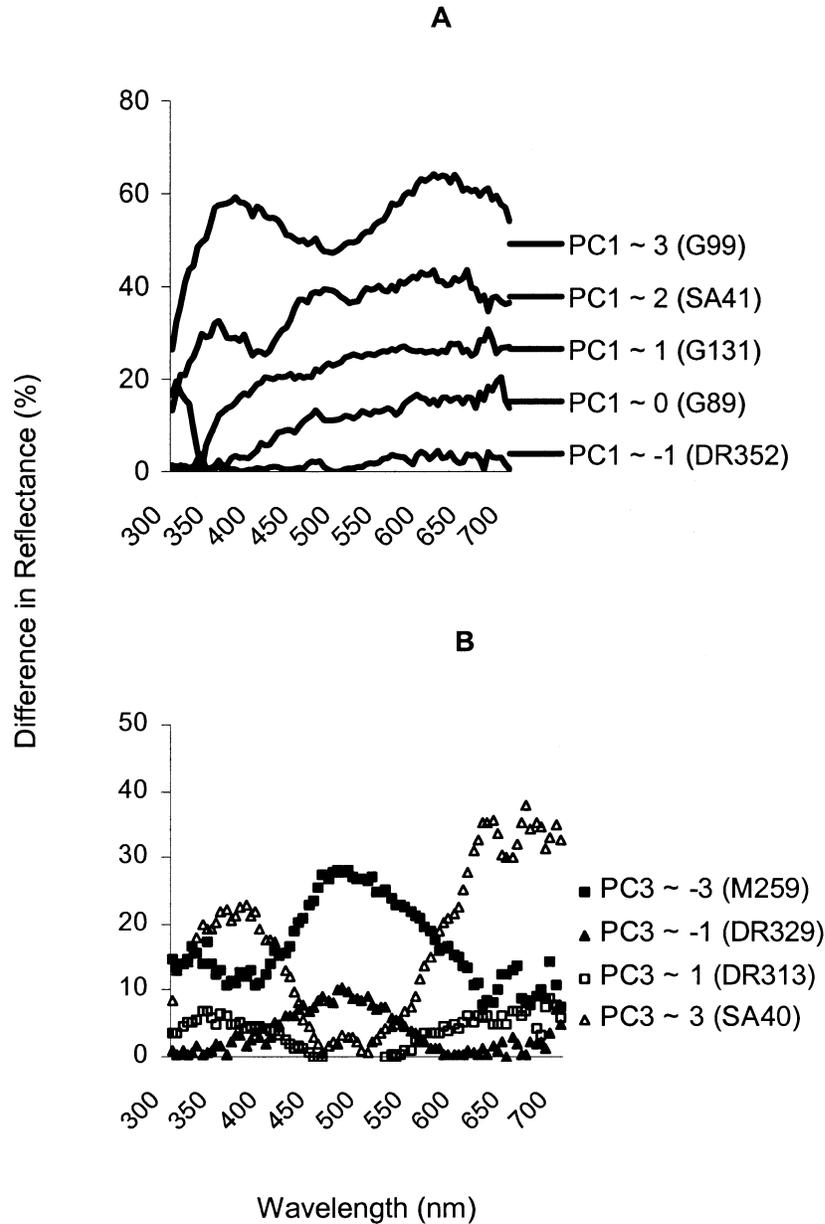


FIG. 4. Relationship of PC1 (A) and PC3 (B) values to sample spectral differences between host and experimental eggs. Each line represents reflectance differences across the spectrum between a given host egg and parasitic egg. As the PC1 value increases, the difference in average reflectance increases. As the PC3 value increases, the intensity of blue-green reflectance decreases relative to reflectance at other wavelengths.

sity, color, and the degree of aggregation at the cap (broad end of the egg). I ranked each spotted egg in the field into one of three categories for each variable. After the experiment I obtained quantitative measurements to indicate the continuous scale of measurement underlying the categorical variables. For spot size, density, and cap aggregation, 16 representative eggs were measured per level, four from each population. For spot color, reflectance spectra of spots were obtained for five representative eggs per level. For all variables, the qualitative ratings for each level corresponded consistently to a range of quantitative measurements that did not overlap with other levels.

I calculated the difference between host and experimental

eggs in each spotting variable (color, size, density, and cap aggregation) as the difference between the categorical values (range 0–3). Differences of 0, 1–2, and 3 in these variables were partitioned as three levels of a categorical variable to achieve similar sample sizes across levels.

I also took note of colony size, nest height, clutch size, and whether the host female was finished laying at the start of the experiment, to test for possible associations with egg rejection.

Statistical Analysis

I used logistic regression (LR; Hosmer and Lemeshow 1989; see also Jackson 1998), with SYSTAT 10.0 software

TABLE 1. Results of a four-population combined logistic regression model demonstrating that village weavers (*Ploceus cucullatus*) reject foreign eggs on the basis of egg color, spotting, and clutch completion. Color and spotting predictors refer to the difference between host and foreign (experimental) eggs. The estimate is the value of the coefficient in the logistic regression equation; it is presented with its associated standard error and *P*-value. For color variables, the odds ratio (with its associated 95% confidence interval) is the average factor by which egg rejection increases for a one unit increase in the predictor variable (PC). For spot density, the odds ratio is the likelihood of rejection at low or medium spot density differences relative to high difference (see text for interpretation of levels). For egg laid during experiment, the odds ratio is the factor by which rejection is more likely when the host has already completed her clutch than when she is still laying during the experiment.

Predictors	Estimate	SE	Odds ratio (95% CI)	<i>P</i>
(Constant)	0.63	0.38		0.09
PC1 (brightness)	0.63	0.14	1.88 (1.44–2.46)	<0.00001
PC3 (visible hue/chroma)	0.44	0.13	1.56 (1.20–2.01)	0.001
Spot density (low)	-2.22	0.35	0.11 (0.06–0.21)	<0.00001
Spot density (medium)	-1.21	0.37	0.30 (0.15–0.61)	0.001
Egg laid during experiment	0.89	0.31	2.44 (1.32–4.52)	0.005

(SPSS Inc., Chicago, IL) to relate predictor variables to the incidence of egg rejection and to compare rejection behavior across populations. As described in Hosmer and Lemeshow (1989), appropriate models were chosen based on log-likelihood values, and fits of these models were assessed by two methods: by McFadden's rho-squared (ρ^2), and with measures of sensitivity (*Sns*) and specificity (*Spc*) provided by SYSTAT 10.0. The ρ^2 -value estimates explained variation like the R^2 of linear regression, but systematically returns much lower values than R^2 ; values between 0.20 and 0.40 are considered satisfactory (Hensher and Johnson 1981). *Sns* and *Spc* capture the overall utility of the model for prediction. *Sns* is the probability that the model would accept the true value of the response variable (i.e., egg rejection) given the values of the predictor variables; and *Spc* is the probability that the model would reject a false value of the response variable. Differences among populations in rejection behavior were tested by looking for significant population by trait interactions. Hypotheses were tested at the $P < 0.05$ level of significance.

Comparisons between Studies

I reanalyzed a portion of my data from Hispaniola in an attempt to replicate the methods of prior studies on this population (Cruz and Wiley 1989; Robert and Sorci 1999). Like Cruz and Wiley (1989), I compared rejection rates of hosts whose eggs were different versus the same as the foreign eggs in the presence or absence of spots. Since Cruz and Wiley (1989) used approximately the mean egg color for the population in all replacements, I excluded data where the difference in color between host and experimental eggs was more than half the population range. Like Robert and Sorci (1999), I divided egg comparisons into two categories, mimetic and nonmimetic, on the basis of difference in color and spotting. Following Robert and Sorci (1999), these categories were distinguished by visual inspection of the eggs. All such determinations were performed in the field before the experiments began. Data were excluded if color or spotting differed but not both. Eggs painted colors not found on Hispaniola were excluded from both analyses.

This replication is imperfect for at least three reasons. First, artificial eggs were used in prior studies but not in the present one. Second, Robert and Sorci (1999) introduced two foreign eggs to each nest (one an artificial cowbird egg), whereas

Cruz and Wiley (1989) and I introduced only one. Both of the prior studies report that these two factors did not influence their results. Finally, the earlier studies described egg color subjectively, so the degree of egg color differences in prior studies bears an uncertain relationship to the spectral data presented here.

RESULTS

Egg Rejection Controls

No eggs were rejected in 43 of 45 surviving control nests in all populations combined, suggesting that our manipulation did not have a strong effect on the rejection behavior of hosts. Eggs painted to mimic host eggs on Hispaniola were accepted in 15 of 16 additional control nests, indicating that paint was an adequate substitute for natural coloration for egg recognition purposes, and that a lack of mimicry in UV wavelengths did not often lead to rejection. This result is corroborated by the nonsignificance ($P = 0.6$) of paint as a variable in a logistic regression model predicting egg rejection on the basis of difference in color.

Predictors of Egg Rejection

In the combined analysis of all four village weaver populations, four variables were significant predictors of rejection: the difference between foreign and host eggs in (1) brightness (PC1); (2) difference in visible hue/chroma (PC3); (3) difference in spot density; and (4) whether or not the host female was still laying during the experimental period (LR: $N = 348$, $P < 0.00001$, $\rho^2 = 0.216$, $Sns = 0.61$, $Spc = 0.66$; Table 1). The most parsimonious model was chosen based on a comparison of ρ^2 -values when variables were added or subtracted. The same four variables and only these variables were also significant ($P < 0.05$) in a full model. No population interactions were included in the most parsimonious model, so results below are presented for all populations combined.

The likelihood of hosts rejecting parasitic eggs increased with greater differences in brightness, visible hue/chroma, and spot density between host and experimental eggs. PC1 characterized the difference in spectral brightness between host and experimental eggs as ranging from -1 to 4. According to the optimal logistic regression model, the value of 1.81 (95% CI: -0.08, 4.31) was the LD50, or the value

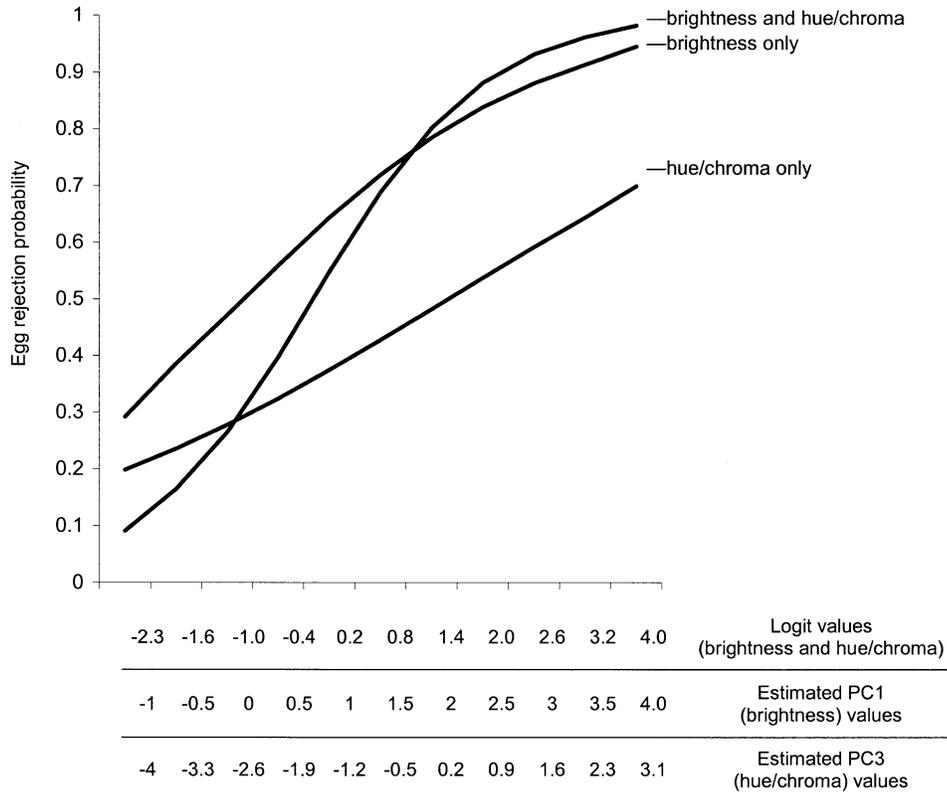


FIG. 5. Rejection of foreign eggs by village weavers according to difference in color between host and experimental eggs. Each line is a logistic regression model based solely on color measurements (PC1, brightness; PC3, hue/chroma; or both), from all four populations combined. These models are poorer than the multivariate one presented in the Results (see Table 1), but they demonstrate that using both brightness and chroma allows birds to better avoid both acceptance and rejection errors than if they used only one of these two aspects of color.

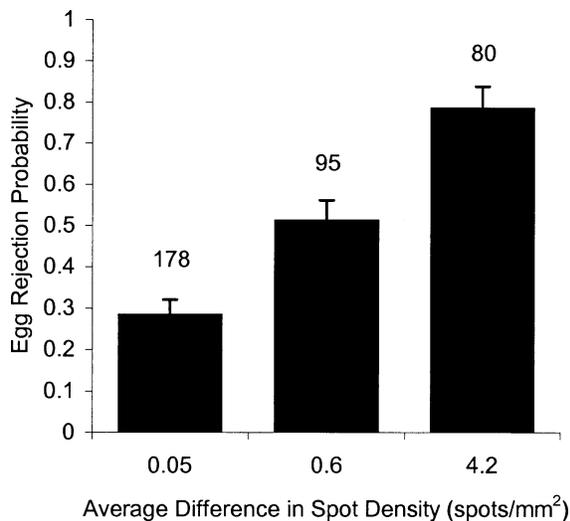


FIG. 6. Rejection of foreign eggs by village weavers according to difference in spot density between host and experimental eggs. Data are categorical, from all populations combined; quantitative values are estimates based on indexing from representative eggs in each category. Raw results (regardless of the effects of other predictor variables) are displayed for ease of graphical representation; see text for relative differences of rejection between spot density levels when corrected for the effects of other variables. Numbers above the columns are sample sizes. Bars are standard errors.

at which an experimental egg would be rejected with 50% probability if all other egg appearance features did not differ. The difference in hue/chroma as measured by PC3 ranged from -4 to 3 , and the LD50 was 0.00 (95% CI: $-2.05, 2.35$). For graphical representations of egg rejection probability in a model based on differences in color alone, see Figure 5. The optimal model predicts an increase in rejection probability of 0.13 for foreign eggs that differed from the host's by an average of 0.6 spots/mm² and an increase of 0.30 for a difference of 4.2 spots/mm², if all other egg appearance features are held constant. All spotting variables were found to be correlated (Spearman correlation 0.69 – 0.76 , $N = 353$), so although other spotting variables (spot color, size, and aggregation) were not significant when spot density was in the model, spot density is probably not the only spot characteristic used by village weavers for recognition and rejection of foreign eggs. For the uncorrected effect of spot density on egg rejection, that is, regardless of the contribution of other predictor variables, see Figure 6.

Finally, birds were on average 2.44 times more likely to reject an egg if they had completed their clutch before the experimental egg replacement occurred. Even without correcting for other variables in the model, 51% of experimental eggs ($N = 139$ of 273) were rejected from nests in which laying was complete before the experiment began; whereas 32% of experimental eggs ($N = 26$ of 81) were rejected from

TABLE 2. Egg rejection by village weavers on Hispaniola: results of the replication of Cruz and Wiley (1989). Descriptions in the left column are of the differences between host and experimental eggs. Data are from conspecific eggs from the Dominican Republic (63 cases in Cruz and Wiley, and 81 cases from this study), and artificial eggs designed to look like village weaver eggs (49 cases in Cruz and Wiley). In both datasets, egg color differences between host and foreign eggs were random, but limited to half of the population range. The degree of spotting of spotted experimental eggs was random, reflecting population variability.

	Accepted	Rejected	<i>N</i>	Rejection
Data from Cruz and Wiley 1989				
Both eggs spotted	36	4	40	
Both eggs plain	17	3	20	
Total (eggs similar)	53	7	60	11.7%
Host egg plain, foreign egg spotted	18	4	22	
Host egg spotted, foreign egg plain	26	4	30	
Total (eggs different)	44	8	52	15.4%
Data from this study				
Both eggs spotted	30	3	33	
Both eggs plain	27	1	28	
Total (eggs similar)	57	4	61	6.6%
Host egg plain, foreign egg spotted	5	1	6	
Host egg spotted, foreign egg plain	12	2	14	
Total (eggs different)	17	3	20	15.0%

nests in which at least one additional egg was laid during the experiment.

None of the following variables approached significance as predictors of egg rejection: egg shape, egg mass, colony size, nest height, or clutch size. PC2 and PC4, two variables that represent differences in near-UV reflectance, also were not significant.

Population Differences in Egg Rejection

If the evolution of egg appearance is not controlled and experimental eggs for each population are a random subset of conspecific eggs from that population, mean rejection rate of experimental eggs differing in appearance (*sensu* Cruz and Wiley 1989; see Materials and Methods) from host eggs was higher in South Africa (65%, $N = 42$) than on Mauritius (55%, $N = 32$), and higher in The Gambia (55%, $N = 38$)

than on Hispaniola (15%, $N = 20$). The difference is not significant for Mauritius (χ^2 : SA_s vs. M_i: $P = 0.24$) but is for Hispaniola (G_s vs. H_i: $P = 0.003$).

A better test for population differences in egg rejection behavior comes from the larger dataset in which egg appearance evolution was controlled. In the combined four-population model presented in Table 1, there were no significant interactions with population (in all cases, $P > 0.1$, ρ^2 increases by < 0.02 when interaction terms are added; $N = 93$ for SA_s, 51 for M_i, 71 for G_s, 133 for H_i).

Adding the interaction between population and difference in brightness to the model indicates a slight difference in the effect of brightness (PC1) among populations. The interaction is excluded from a parsimonious model because the improvement to prediction is minimal, for a large cost in degrees of freedom (G -test: 10.55, $df = 6$, $P = 0.10$; ρ^2 increases by 0.02, Sns by 0.008, Spc by 0.006). Analysis of models of all two-population pairs confirms that this effect is due to a difference between South Africa and other countries (SA_s vs. M_i: $P = 0.03$; vs. H_i: $P = 0.03$; vs. G_s: $P = 0.14$. All other pairs: $P > 0.25$). Specifically, the effect of difference in brightness (PC1) on rejection was lower in South Africa than in the other populations.

Comparisons between Studies

Combined results from experiments with artificial and natural village weaver eggs on Hispaniola from Cruz and Wiley (1989) indicate 11.7% (seven of 60) rejection of experimental eggs that are similar to host eggs in the presence or absence of spotting. When eggs differed in the presence or absence of spots, 15.4% of eggs (eight of 52) were rejected. Their methods resulted in all eggs differing randomly in color as well, up to half of the population range. With similar criteria applied in the present study, such that a subset of my data was analyzed, the percentages of eggs rejected are 6.6% (four of 61) and 15.0% (three of 20), respectively (Table 2).

Artificial eggs placed into Hispaniolan weaver nests by Robert and Sorci (1999) were rejected 16.0% of the time (four of 25) when they were judged not to differ in color and spotting from host eggs, whereas they were rejected 67.5% of the time (27 of 40) when they were judged to differ in color and spotting. In the present study similar assessments were made, and the respective rejection percentages were 8.8% (three of 34) and 64.3% (18 of 28; Table 3).

TABLE 3. Egg rejection by village weavers on Hispaniola: results of the replication of Robert and Sorci (1999). Descriptions in the left column are of the differences between host and experimental eggs. Data from Robert and Sorci are from artificial eggs designed to look like village weaver eggs; an artificial cowbird egg was also introduced with the artificial weaver eggs in many cases. Data from this study are from conspecific eggs, some of which were painted colors found among natural eggs on Hispaniola. The similar versus different distinctions in Robert and Sorci and in this study were based on subjective estimations in the field before the experiments were concluded. Robert and Sorci did not remove host eggs during the experiment, but one host egg was removed from each nest in this study.

	Accepted	Rejected	<i>N</i>	Rejection
Data from Robert and Sorci 1999				
Eggs similar in color and spotting	21	4	25	16.0%
Eggs different in color and spotting	13	27	40	67.5%
Data from this study				
Eggs similar in color and spotting	31	3	34	8.8%
Eggs different in color and spotting	10	18	28	64.3%

Rejection Costs

Among experimental nests from which a foreign egg was rejected, a host egg was also rejected from 15% of nests (22 of 146) across all populations. This sample excludes 39 one-egg clutches: because methods involved removing a host egg, birds had no opportunity to reject their own egg in those cases. These costs of rejection were higher in the source populations than in the introduced populations, and this difference was significant for the older introduction (χ^2 : G_s [41%, 13 of 32] versus H_i [6%, three of 48], $P = 0.0002$; SA_s [12%, five of 41] vs. M_i [4%, one of 25], $P = 0.26$). In only one case (on Hispaniola) did a bird reject her own egg but leave a foreign egg in the nest.

DISCUSSION

Dynamics of Rejection Behavior upon Release from Cuckoo Brood Parasitism

When challenged with experimental brood parasitism, village weavers in all four study populations rejected foreign eggs in proportion to the difference in color and spotting between those eggs and their own. Weaver populations introduced to areas without egg-mimicking brood parasites have higher within-clutch variation and lower between-individual variation in egg appearance features used in recognition (Lahti 2005). A simple comparison of conspecific egg rejection rates in each population illustrates that the introduced weavers are less successful at rejecting parasitic conspecific eggs from their own population, an effect that is statistically significant for the older introduction (Hispaniola) but not for the more recent one (Mauritius). If these populations were to re-establish sympatry with the diederik cuckoo, they would likely reject fewer eggs and suffer a higher rate of successful parasitism as compared to the currently parasitized populations, particularly by cuckoos that happened to match Hispaniolan weaver egg colors.

When the effects of short-term evolutionary changes in the appearance of weaver eggs are controlled, however, neither introduced population differs from its source population in the likelihood of a female rejecting a foreign egg of a given difference in color and spotting from her own eggs. The lower frequency of egg rejection in the introduced populations can therefore be attributed to a decline in visual signature information. Declines in rejection behavior have previously been interpreted as stemming from changes in the abilities of birds to distinguish differences in egg appearance and to reject different eggs from their nests. This study detected no change in these abilities in village weavers. Thus, if the ancestral population variation and clutch uniformity in egg color and spotting were restored to the introduced populations, as this study roughly approximated experimentally and statistically, we would be unlikely to detect a decline in rejection behavior on Mauritius relative to South Africa or on Hispaniola relative to The Gambia. This interpretation is supported by the absence of population interactions in both the combined model and two-population comparisons.

Costs of rejection (own eggs rejected with the foreign eggs) were evident but varied across populations. The decrease in such costs between The Gambia and Hispaniola is contrary

to what might be expected if birds had lost efficiency in their rejection response in the absence of the cuckoo. The incidence of rejection errors does not correlate with any measured egg appearance, experimental, or environmental variables. One possibility is that ease of egg rejection depends on nest construction; this differs across populations and is influenced perhaps by variation in materials, weather, predators, and extent of brood parasitism (e.g., Lahti et al. 2002). If nests in the region of cuckoo parasitism have narrower or longer entrance tubes, deeper nests, or higher thresholds to foil cuckoos, recognition or rejection could be more difficult in those areas.

The finding that introduced weavers retain their ability to reject eggs suggests that environmental features that differ between source and introduced populations do not significantly influence egg rejection behavior in this species. In particular, the diederik cuckoo was present and singing at study sites in The Gambia and South Africa, but its absence from Hispaniola and Mauritius apparently did not reduce the expression of rejection behavior. Stimuli associated with actual cuckoo parasitism events might increase the likelihood of egg rejection, but this study did not test for effects of interactions with an adult cuckoo at the host nest.

Egg recognition has persisted in the introduced village weaver populations in spite of the fact that the predominant selective agent rendering it adaptive is missing in the introduced populations. Patterns of egg appearance evolution in the introduced populations imply that egg appearance variability and egg rejection behavior in the ancestral populations have been maintained by diederik cuckoo parasitism (Lahti 2005). Egg recognition in the village weaver has persisted despite lost functionality in another sense as well: it has lost some potential functionality due to the decay of other components in a functionally integrated suite of traits. Evolution of egg appearance in the introduced populations has decreased the uniformity and distinctiveness of weaver clutches, thereby reducing the potential effectiveness of egg recognition were the birds again subjected to an egg-mimicking parasite.

The only brood parasite on Hispaniola is the shiny cowbird (*Molothrus bonariensis*; Post and Wiley 1977), which expanded into the Greater Antilles during the last few decades. I observed no shiny cowbird parasitism of village weavers, but such parasitism has been observed in the past when the cowbird was apparently more common on the island (Cruz and Wiley 1989; J. Wiley, pers. comm.). Shiny cowbird eggs are white and spotted (Biaggi 1983; Cruz and Wiley 1989) and are far different from the appearance of any weaver eggs on Hispaniola. Rejection of shiny cowbird eggs does not require the village weaver's refined level of egg recognition ability, and so is unlikely as an explanation for the persistence of egg recognition.

Egg recognition and selective rejection of foreign eggs might be somewhat functional in the introduced populations as a defense against conspecific brood parasitism. Several weaver species are known to parasitize conspecifics (Freeman 1988; Jackson 1992), although I did not observe conspecific brood parasitism in my study populations. Enough within-clutch uniformity and between-individual variation persists in Mauritian and even Hispaniolan weavers to allow rejection

of some conspecific eggs (see Tables 2, 3). If conspecific parasitism avoidance were maintaining egg recognition ability in the introduced populations, we would expect it also to maintain the egg appearance traits that make egg recognition possible. In fact, those egg appearance traits have decayed, in proportion to the time since divergence from the ancestral population (Lahti 2005). Thus, selection imposed by conspecific parasitism in village weavers is apparently minimal, relative to selection imposed in the source populations by the diederik cuckoo.

I propose two mutually compatible hypotheses for the persistence of egg recognition in the introduced populations. First, recognition abilities may have low cost and may not be subject to the same strength of negative selection as are egg color and spotting; in particular, rejection behavior might simply remain unexpressed, whereas egg pigmentation is always expressed. Second, recognition systems may be more pleiotropic than egg color and spotting; egg recognition ability might be maintained, for instance, because it has the same neural basis as other perceptual and cognitive functions that are still important in the introduced populations (see Basolo and Endler 1995). In contrast, the pigment epithelium of a bird's shell gland has no known function other than to deposit pigment on eggshells.

Factors Influencing Egg Rejection

As reported previously for the Gambian population alone, color and spotting of egg shells, but not egg size, egg shape, or microhabitat, provided cues for rejection of foreign eggs by village weavers. This result is predicted from an analysis of the relative reliability of different egg features as signature cues (Lahti and Lahti 2002; see also Victoria 1972; Jackson 1998). Difference in overall brightness between host and parasite eggs had the greatest influence on egg rejection, although birds also used hue or chromatic differences. As indicated by tests with painted eggs that mimicked natural eggs in the human-visible range, lack of UV reflectance in foreign eggs by itself was not sufficient to elicit egg rejection. Likewise, two principal components related to variation in the UV reflectance had no significant effect on egg rejection, although a more focused study would be required to test whether UV reflectance plays any role in egg recognition.

In contrast to the other three populations, South African weavers did not rely as strongly on brightness to distinguish foreign eggs, perhaps reflecting differences in perceptual ability in different light environments. Experiments in South Africa were initiated under cloud cover and during rain more frequently (61% of nests, 70 of 115) than experiments in the other study areas (M_i zero of 56; G_s 23%, 13 of 57; H_i 7%, 10 of 149), where nests were usually in full sun most of the day. Differences in chroma and hue of eggs should be more conspicuous than differences in brightness under overcast skies (see Endler 1993).

Foreign eggs were not as likely to be rejected within 48 h if they were introduced during the laying period, as they were if introduced afterward. There were no significant interactions with egg appearance, so the birds that delayed rejection did not do so because they were parasitized with similar eggs to their own. Perhaps the ability to view one's

complete clutch aids in egg recognition, especially for younger birds that are still in the process of learning the appearance of their eggs (Lotem et al. 1995). Victoria (1972) observed that village weavers frequently adjust the position of their eggs from the time they lay their first one. This behavior may help familiarize the birds with the visual image of their eggs and facilitate egg recognition in the event of parasitism.

All significant predictors together produced a highly significant model with a moderate level of predictive power comparable to that in other evolutionary studies (Møller and Jennions 2002; e.g., *Sns* and *Spc* values in the 0.60–0.70 range even with other, marginal, variables included). It is likely that variables not considered in this study also influence egg rejection behavior. Moreover, like Victoria (1972), after hundreds of egg replacement experiments I could in most cases predict a priori whether an egg would be rejected or accepted, which suggests that my methods of assessing color and spotting, though extensive, do not fully capture the integration of visual stimuli in a bird (or human) brain. The fact that the more subjective color chart data produced results with higher significance values than spectrophotometry (see Materials and Methods) also suggests this interpretation. Research on bird song encounters similar difficulties (Payne et al. 2000). An additional source of variation in my data may be differences in the prior experience of individual hosts. Experiments with other cuckoo hosts suggest that older individuals may be more effective at recognizing and rejecting foreign eggs (Rothstein 1974; Lotem et al. 1992, 1995).

Replication of Prior Studies

I replicated the methods of both Cruz and Wiley (1989) and Robert and Sorci (1999) and observed similar egg rejection rates to those found in the original studies, suggesting that my approximation of their methods was adequate and that differences among studies in observed rates of conspecific egg rejection in Hispaniolan weavers can be attributed to differences in methodology. More importantly, this study suggests that the ability of Hispaniolan weavers to reject eggs that differ in appearance from their own has not changed appreciably since 1974—and indeed since they were introduced.

This finding has several implications. The low levels of conspecific egg rejection reported by Cruz and Wiley (1989) were due to two factors: their choice of experimental eggs and the evolution of egg appearance in Hispaniolan weavers. Cruz and Wiley (1989) were correct in concluding that the frequency of egg rejection behavior had declined but incorrect in their assumption that the recognition system had declined. Rather, changes in within-clutch and between-individual variation in egg appearance reduced the effectiveness of egg recognition as compared to the ancestral African population. Similarly, the rapid increase in egg rejection behavior subsequently reported by Robert and Sorci (1999) is an artifact of the somewhat different methods they used as compared to Cruz and Wiley (1989). The higher levels of rejection behavior observed by Robert and Sorci (1999) are most likely due to the fact that their methods for choosing experimental eggs captured more (probably all) of the population variation

present on Hispaniola, whereas the methods of Cruz and Wiley (1989) captured only a small subset of this variation.

Cruz and Wiley (1989) also found low levels of weaver rejection of shiny cowbird eggs. As mentioned above, rejection of these eggs, as with rejection of *Molothrus* cowbird eggs by other hosts, is not likely to be influenced by difficulties in recognition. Levels of rejection of cowbird eggs are likely explained by other issues, such as the physical difficulty of rejecting eggs and the fitness costs and benefits of rejecting them (see Rothstein 1990).

Future studies of the evolution of eggs and egg rejection in hosts of brood parasites should quantify differences in appearance between host and experimental eggs and analyze the likelihood of egg rejection as a function of these differences. The use of a simple rejection rate, that is, the percentage of eggs rejected versus accepted (even when compared for mimetic and nonmimetic eggs), is not appropriate for a brood parasite–host system where either the host or the parasite has eggs with variable colors or spotting patterns.

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