



## How precise is egg discrimination in weaverbirds?

DAVID C. LAHTI & APRIL R. LAHTI

Department of Biology and Museum of Zoology, University of Michigan

(Received 3 August 2000; initial acceptance 19 December 2000;  
final acceptance 20 November 2001; MS. number: A8847R2)

The village weaverbird, *Ploceus cucullatus*, lays eggs of an extremely broad range of appearance between individuals. This variation is thought to have evolved as a counteradaptation to brood parasitism by the diderik cuckoo *Chrysococcyx caprius*. The primary objective of our study was to characterize the relationship between egg appearance and egg rejection in the African village weaverbird. We test predictions of three hypotheses in a study in The Gambia, West Africa: (1) interindividual egg variability permits individuals to discriminate between own and foreign eggs by rejecting eggs in proportion to the difference in appearance from their own; (2) village weavers remember the appearance of their own eggs and do not require a discordancy within their clutch, nor even the presence of one of their own eggs, in order to distinguish a foreign egg as such; and (3) colour and speckling contain the signature information by which village weavers can distinguish their eggs from foreign ones; whereas shape and mass, being less reliable, do not. We analysed rejection behaviour according to egg appearance differences by logistic regression. Results supported all three hypotheses. We estimated the predictive efficacy of our model, the amount of explained variation and the relative contribution of various egg appearance factors to discrimination by the host. These results are consistent with the hypothesis that interindividual egg variation in this species facilitates offspring recognition and is a counteradaptation to either interspecific or intraspecific brood parasitism.

© 2002 The Association for the Study of Animal Behaviour. Published by Elsevier Science Ltd. All rights reserved.

The cost to a parent of raising another's offspring often makes the discrimination of its own from other offspring worthwhile (Beecher 1991). Often parents effectively discriminate by following simple rules of thumb, perhaps relating to their history of copulation or location of the offspring (Davies et al. 1992). However, sources of parental uncertainty such as extrapair copulation and brood parasitism can decrease the reliability of such rules. For instance, in a species that is subject to interspecific brood parasitism by a cuckoo that mimics host eggs, natural selection is expected to favour more elaborate means of offspring (here egg) discrimination (Payne 1997), such as the comparison of the offspring's 'signature information' with some standard (Beecher 1991; Davies 2000). In these cases, certain cognitive faculties may become well developed, including memory for offspring appearance and the ability to distinguish relevant differences. A complementary evolutionary strategy would be the production of offspring that are more distinctive, thereby facilitating recognition.

Several studies have demonstrated that certain hosts of brood parasitic cuckoos do treat egg characteristics as

signatures to some extent, and reject foreign (usually model) eggs that are sufficiently dissimilar to their own (e.g. Davies & Brooke 1989; Moksnes 1992; Lotem et al. 1995). Egg rejection rate in one population was negatively correlated with variation within an individual's own clutch (Stokke et al. 1999), which demonstrates the importance of reliability in signature information. A comparative analysis suggests that this trend, together with a positive correlation of egg rejection rate with interclutch variation, may be true of European passerines subject to brood parasitism as a whole (Soler & Møller 1996). More direct evidence that egg rejection can function as a defence against brood parasitism is provided by studies that found egg rejection rates to correlate with the likelihood of cuckoo parasitism spatially (Davies & Brooke 1989; Soler et al. 1999; Lindholm & Thomas 2000), or temporally (Brooke et al. 1998; Nakamura et al. 1998). Few studies, however, address the question of how precise egg discrimination is in species that reject foreign eggs. How nonmimetic does an egg have to be before it is rejected by a host? Or, conversely, what is the range of appearance over which a host will accept an egg? This question is perhaps most complex and interesting in the context of hosts that lay eggs of a wide variety of appearance between individuals, such as the *Ploceus* weaverbirds (Moreau 1960). In these species a cuckoo

Correspondence: D. C. Lahti, Museum of Zoology, University of Michigan, Ann Arbor, MI 48109-1079, U.S.A. (email: lahtid@umich.edu).

cannot effectively mimic an entire population's eggs, but only a subset of them. In addition, conspecific brood parasitism may be occurring in several *Ploceus* species (Freeman 1988). Individuals are likely, therefore, to be presented with foreign eggs that are at various points on a continuum of mimesis. This situation provides an opportunity for experimental tests to determine the relationship between degree of mimesis and probability of egg rejection (Jackson 1998).

Interindividual variation in egg appearance in the village weaver *Ploceus cucullatus* is among the highest of any bird (Moreau 1960; Schönwetter 1983). An individual female, however, lays eggs of a characteristic colour and speckling pattern throughout her life. Collias (1984) collected all eggs laid by nine village weaver females over 2–9 years, and assessed the colour of their eggs according to the same charts used in this study (see Methods). For the average bird, 65.5% of eggs were the same shade of lightness and chromaticity, 18% differed by one shade in either of these dimensions, and the remaining 16.5% differed by more than one shade. In contrast to this similarity within an individual over her lifetime, even neighbouring birds in a colony can lay eggs of widely differing appearance. Among eggs from 137 nests in our study site (using percentage data to facilitate comparison with Collias 1984) only 1% were the same shade of lightness and chromaticity as the average egg, and 12.4% differed by one shade in either of these dimensions.

A study of a small number of individuals in a captive population (Victoria 1972) found that female weavers reject dissimilar eggs of their own species from their nests, although the study did not include statistical analysis or quantification of egg appearance. In the natural range of this species in Africa, the diderik cuckoo *Chrysococcyx caprius* parasitizes the village weaver and other species (Morel & Morel 1962; Maclean 1993). The diderik cuckoo eggs laid in village weaver nests are mimetic of the species in general (Payne 1967), although the difference between a village weaver's own eggs and a cuckoo egg laid in the nest will be somewhere on a continuum due to high interindividual host egg variability. If accepted, the cuckoo egg generally hatches first, and any remaining host eggs are removed by the diderik nestling (Hunter 1961; Reed 1968). How diderik cuckoos choose host nests is still unknown.

The primary objective of our study was to characterize the relationship between egg appearance and egg rejection in the African village weaver. We hypothesize first that interindividual egg variability permits individuals to discriminate between own and foreign eggs by rejecting eggs that differ in appearance from their own. Specifically, we predict that foreign eggs will be rejected in proportion to their difference in appearance from host eggs. Addressing this hypothesis allows us to test an assumption in the literature regarding the evolution of egg rejection in this species. Cruz & Wiley (1989) argued that in an introduced population on the Caribbean island of Hispaniola, the village weaver's behaviour of rejecting dissimilar eggs had declined, because of the absence of brood parasites in that region. Subsequently, Robert & Sorci (1999) reported a rapid recovery of

rejection behaviour in the same population, and attributed this to recent colonization of the weavers by the brood parasitic shiny cowbird, *Molothrus bonariensis*. Cruz & Wiley (1989) and Robert & Sorci (1999) assume that the parental population in West Africa has a significant level of egg discrimination and rejection ability.

Discrimination between host and foreign eggs requires a mechanism for host egg recognition. Rothstein (1975) distinguishes two hypothetical mechanisms: recognition by discordancy and true recognition. By the first mechanism, the host bird does not learn the appearance of its own eggs, but treats the more common egg type in the clutch as its own. This permits discrimination against odd eggs, which are more likely to be parasitic. In West Africa where we conducted our study, the clutch size of the village weaverbird is usually either one or two (94% of nests in this study). Since we, as well as the diderik cuckoo, replace eggs rather than adding to a clutch (see Methods), recognition by discordancy is not available to these birds. If village weavers require an outnumbered egg in the clutch in order to distinguish own from foreign eggs, we expect no consistent rejection of foreign eggs in this population. By Rothstein's second mechanism, true recognition, the host bird learns the appearance of its eggs and uses this information to distinguish own from foreign eggs. We divide this mechanism further into recognition by direct comparison, where birds recognize their own eggs when they see them and discriminate against differing eggs by comparing them to their present eggs; and recognition from memory, where birds remember the appearance of their eggs and reject differing eggs by comparison with their memory rather than with their actual eggs. Our prediction is that village weavers will reject foreign eggs at the same rate whether or not their own eggs are also in the nest, which would be consistent with recognition from memory. This mechanism is suggested by Victoria (1972). If, on the contrary, the presence of one of their own eggs in the nest aids a village weaver in distinguishing a foreign egg as such, this suggests that the mechanism of recognition by direct comparison is being used to some extent.

Shape and mass are much less consistent within an individual than are colour and speckling (Collias 1984). Therefore, our third hypothesis is that colour and speckling contain the signature information by which village weaver parents can distinguish their eggs from foreign ones; whereas shape and mass, being less reliable, do not. In accordance with this hypothesis we predict a positive relationship between egg rejection and differences in colour and speckling between host and foreign eggs, and no relationship between egg rejection and differences in shape and mass.

## METHODS

### Study Site and Study Animals

We conducted the experiment on and around Georgetown (Janjangbureh) Island (13°33'N, 14°46'W) in The Gambia, West Africa during the breeding season of the village weaver and the diderik cuckoo (July–August

1999). Wetmore & Swales (1931) identified the form of the village weaver in this region of Africa as that which was introduced into Hispaniola. Diederik cuckoos were heard and seen in the study area over the course of the experiment, but no incidence of parasitism was known to have occurred among our study nests.

The African village weaver is a common passerine with a polygynous mating system that builds elaborate, enclosed nests in often dense colonies (Barlow et al. 1997). Each male builds several nests in the course of a breeding season. The female chooses a nest, lines it, and incubates a clutch of eggs for 12 days, during which time the male does not enter the nest (Collias & Collias 1970; Da Camara-Smeets 1982). Among our study nests ( $N=143$ ), clutch size was usually two (71.3%), but sometimes one (22.4%) or three (6.3%). We most commonly found colonies in palms and acacias along the banks of the Gambia River, and in tall trees near the centres of towns and villages (Lahti et al., in press). We experimented on nests in 13 colonies or nest aggregations, ranging from 12 nests to an estimated 400. The nests in these colonies ranged from 0.6 to 10.7 m in height, which was also the range of our study nests ( $\bar{X}=2.6$ ,  $N=143$ ).

## Experimental Parasitism

We parasitized 96 nests with other village weaver eggs, of a variety of colours and speckling patterns, based on the methodology outlined in Rothstein (1975). On each host egg and foreign egg we wrote a number on the cap (broad end) of the egg for identification. In each case we replaced one host egg with a foreign egg, as the diederik cuckoo is known to do (Friedmann 1968). In 35 of our experimental nests, we replaced the only host egg in the nest with the foreign egg. In a further 55 nests there were two host eggs before the experimental period, such that there was still one host egg in the nest after we replaced the other with a foreign egg. In the remaining six nests there were three host eggs, one of which we replaced with a foreign egg. We believe that village weaver eggs are an appropriate experimental substitute for diederik cuckoo eggs. The diederik cuckoo eggs laid in the nests of weavers are effective mimics, so even experienced ornithologists are often unable to tell the difference in the field (Friedmann 1968; Jensen & Vernon 1970; Colebrook-Robjent 1984). We replaced eggs between 0800 and 1200 hours. Study nests were unmarked; a numbered tag was placed at least 1 m from each nest during the experimental period.

Early in the study we checked each nest twice, at 24–28 h and 48–52 h after replacement. After performing this experiment on 42 nests, we found that no rejection occurred between 24 and 48 h, and that most rejection occurred on the same day as the egg replacement. We checked the remaining nests only once, at 24–28 h after replacement. Eggs damaged or missing were considered rejected. All eggs were removed from each nest and measured at the end of the experimental period.

Our methods had negligible impact on the seasonal reproduction of the individuals involved and on the

persistence and activity of the colonies. Village weavers, which are in fact overpopulated and an agricultural pest in West Africa (Lahti, in press), re-nest rapidly after the loss of a clutch, and raise several broods in a breeding season. On average, less than 10% of nests were disturbed from a given colony, and females generally returned to nests to incubate their eggs within 5 min after researchers withdrew.

Because egg rejection has sometimes been found to correlate with embryo age (Lotem et al. 1992), nests were chosen for experimentation in order to parasitize nests whose females were in or near their laying period. Each nest contained at least one egg at the start of the experiment. We assessed embryo age before experimenting on a nest and did not experiment on nests whose eggs were estimated to have been incubated for more than 4 days. Eggs with no or very small embryos were translucent. In a few cases where eggs were not translucent (older eggs, and some with dark colour and speckling), the egg to be replaced was broken open. In these cases we estimated embryo age based on length and physical characteristics (Daniel 1957; Romanoff 1960). These criteria excluded over 80% of the total number of active nests we accessed. Breeding synchrony within colonies reduced our need to disturb nests, and nearly all accessed clutches that failed to meet experimental criteria were returned to their nests for incubation. Each experimental nest was used only once.

We controlled for a possible effect of our accessing and manipulating nests by removing eggs from an additional 20 nests, writing identification numbers on the caps, and returning them to the nests (Lawes & Kirkman 1996). Tags were placed near these nests as well, and nests were checked after the same time period as experimental nests. This also controlled for nest predation, although nest predation events were generally obvious: either several nests in an area were found without eggs and deserted, or nests showed visible signs of entry by predators. The spatial and temporal distribution of control nests was similar to that of experimental nests. To distinguish acceptance from desertion at experimental nests, we observed some females at the nest after the experimental period, and also checked to see whether individuals that were experimentally parasitized during their laying period completed their clutch and continued to incubate their eggs afterwards.

## Measurements of Eggs

We determined egg colour by visual comparison with the *Villalobos Color Atlas* (Villalobos-Dominguez & Villalobos 1947), which has been used to assess egg colour variation and its inheritance in a captive population of village weavers (Collias 1984, 1993). This atlas has a three-dimensional arrangement with a theoretical basis, which facilitates comparison of shades. The three dimensions, which are independent of each other, are hue (the colour of the pigment), lightness or value (the position on a scale from dark to light), and chromaticity or degree

**Table 1.** Quantification of egg speckling variables by indexing

Variable	Measure	Field estimation	Quantitative (index) value
Spot colour	Lightness scale on colour chart	1	15.5
		2	11
		3	6
Spot size	Average spot area (mm <sup>2</sup> )	1	0.14
		2	0.39
		3	0.61
Spot density	Average number of spots/mm <sup>2</sup>	1	0.12
		2	0.67
		3	1.90
Cap aggregation	1 – (density of rest of egg/density of cap)	1	0
		2	0.38
		3	0.65

Field estimations ranged from 0 to 3 by steps of 0.5. Index values represent the mean of three representative eggs for each variable state.

(the attenuation or concentration of the pigment, from weak to strong). For each of 38 hues there are 19 grades of lightness and 12 degrees of chromaticity, and there are 21 neutral shades (black to white). Of the possible shades, 7279 are represented in coloured squares. Although eggs did vary in hue, nearly all study eggs were best matched to a single hue in the atlas (emerald) or to the set of neutral shades. Eggs were therefore compared only on the basis of the remaining variables, lightness and chromaticity. The difference between two eggs' colours was considered as the sum of the differences in lightness and chromaticity.

We assessed four variables relating to egg speckling: spot colour, spot size, spot density and the degree to which spots were aggregated at the cap (broad) end of the egg. Unmarked eggs were assigned a state of 0 for each variable. Eggs with any speckling were assigned values up to 3 for each variable. Representative eggs were later measured to index our estimates to quantitative parameters (Table 1). Spot colour ranged from 4–17 on the lightness scale in the *Villalobos Color Atlas*. Spot size ranged from 0.10–0.90 ( $\pm 0.05$ ) mm in average width. Spot density ranged from 0.1–2.8 ( $\pm 0.05$ ) mm in average distance between a spot and the nearest neighbouring spot; these figures were used to calculate a value of average spots/mm<sup>2</sup> for each egg. Cap aggregation was described by the proportion  $1 - (D_{\text{rest of egg}}/D_{\text{cap}})$ , where  $D$  is the average spot density in spots/mm<sup>2</sup>. This yields a range of 0–1, the two theoretical extremes being eggs whose spots are all on the cap (1), and eggs whose specklings are distributed evenly over the egg (0). Differences in the four speckling measures were kept as separate variables in the analysis. One of us (A.R.L.) performed all egg colour and speckling assessments. Blind reassessments by A.R.L. and independent assessments by D.C.L. suggested that measurements were consistent.

Egg length and breadth were measured to the nearest 0.1 mm with digital calipers. Shape was considered to be the ratio of length to breadth. Mass was measured to the nearest 0.05 g with a spring scale at the end of the experimental period.

## Statistical Analysis

We used logistic regression (Hosmer & Lemeshow 1989), with SYSTAT 7.0 software to relate the number of eggs in the nest and differences in egg appearance characteristics to the instances of egg rejection. The fits of the models were assessed in two different ways: by measures of sensitivity (*Sns*) and specificity (*Spc*) provided by SYSTAT 7.0, and by a measure of reduction in deviance (*R*) as used in Peeters & Gardeniers (1998). *Sns* is the probability that the model would accept the true value of the response variable (here, 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. These measures capture the overall utility of the model at prediction. *R* is the proportion of the variance in the data that is explained by the predictor variables in the model. As no consensus exists as to assessment of explained variation in logistic regression (Mittlböck & Schemper 1999), we provide both *Sns/Spc* and *R* values here. Hypotheses were tested at the  $P < 0.05$  level of significance.

## RESULTS

Of 116 experimental nests, six were destroyed by storms or animals during the experimental period, and one was abandoned after egg predation. Two of our 20 control nests, where eggs were marked and replaced in the same nests, were also destroyed during the experimental period. Of the 18 surviving control nests, all eggs were accepted in 17, indicating that our manipulation of clutches and nests did not significantly impact the probability of egg rejection, and also that the background level of egg disappearance by rejection or predation was low.

### Egg Rejection According to Egg Appearance Differences

According to the full model, the odds of a host rejecting a foreign egg is proportional to the difference in

**Table 2.** Parameters of multiple logistic regression model, predicting egg rejection on the basis of egg colour and speckling differences between host and foreign eggs

Parameter	Estimate	SE	t ratio	Odds ratio (95% CI)*	P	R
(Constant)	-2.21	0.59	-3.71		0.0002	
Egg colour	0.44	0.13	3.45	1.55 (1.21, 1.99)	0.0006	0.19
Spot density†	-0.33	0.35	-0.93	0.72 (0.36, 1.44)	0.3	0.013
Cap aggregation†	-0.22	0.35	-0.63	0.80 (0.40, 1.60)	0.5	0.020
Spot density×cap aggregation	0.79	0.36	2.19	2.20 (1.09, 4.47)	0.028	0.076

\*The odds ratio estimates how much more likely egg rejection is with one unit increase in the parameter. For ease of interpretation, the odds ratios here for the speckling variables are based on a binary coding (difference=0/difference >0).

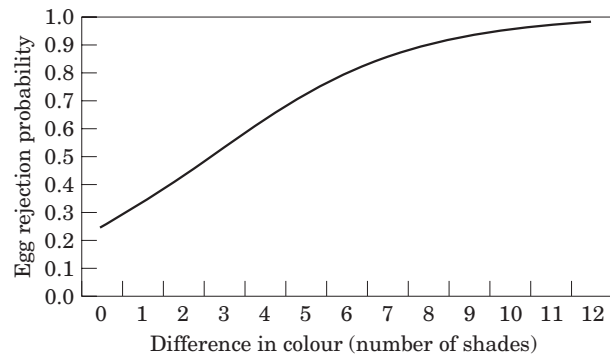
†Main effects were retained, even when nonsignificant, when their interaction was significant.

appearance between the foreign egg and the host's own egg (logistic regression:  $P < 0.0001$ ,  $N = 71$ ,  $Sns = 0.72$ ,  $Spc = 0.79$ ,  $R = 0.36$ ). (This does not imply that there was always a host egg in the nest during the experiment: see Methods.) In univariate analyses, differences between host and experimental eggs in colour and all speckling variables were indicated as potentially important predictors of egg rejection, whereas the number of eggs in the nest and differences in egg shape and mass were not. Moreover, when either the number of eggs in the nest, egg shape, or egg mass were removed from the full model, the significance level and the predictive ability of the model increased. A parsimonious model included the degree of difference in egg colour and the interaction of spot density with spot aggregation at the egg cap (logistic regression:  $P < 0.0001$ ,  $N = 71$ ,  $Sns = 0.63$ ,  $Spc = 0.73$ ,  $R = 0.30$ ; Table 2). In this interaction a response to a difference in spot density was more pronounced when accompanied by a difference in cap aggregation, and vice versa.

The odds ratio was an easily interpretable measure of the parental response to differences in colour and speckling (Table 2). For instance, egg colour difference was a powerful predictor of rejection, with rejection being on average 55% more likely with each additional shade of difference between host and experimental eggs. The odds ratio for the speckling interaction term indicated that an experimental egg was on average twice as likely to be rejected when it differed from the host's egg in speckling than when it was similar. Speckling variables were continuous (Fig. 2), but are represented here as binary solely for convenient interpretation of the odds ratio.

A model including only egg colour differences predicted egg rejection well (logistic regression:  $P < 0.0001$ ,  $N = 71$ ,  $Sns = 0.60$ ,  $Spc = 0.70$ ,  $R = 0.21$ ) (Fig. 1), as did the best model with only speckling variables ( $P < 0.0001$ ,  $N = 71$ ,  $Sns = 0.58$ ,  $Spc = 0.69$ ,  $R = 0.15$ ), although speckling differences explained less of the variance in the response than colour differences. In the combined model, speckling differences explained half as much of the variance as egg colour differences ( $R$ ; Table 2). No significant interaction between colour and speckling variables existed in any model, indicating that the birds assessed colour and speckling independently.

With regard to speckling, multivariate analysis did not suggest that any single variable, or any single interaction,

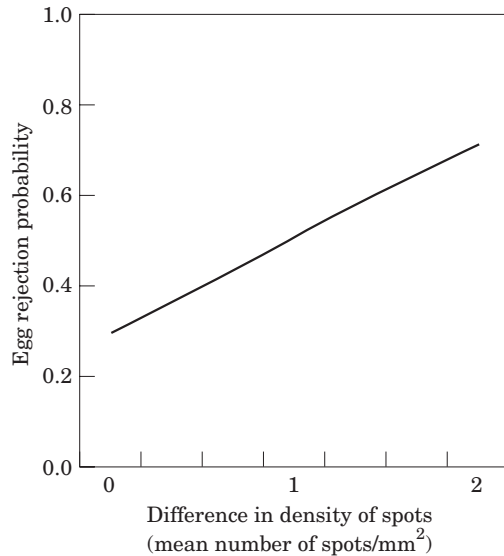


**Figure 1.** Weaverbird rejection of experimental eggs by the difference in colour between host and experimental eggs. The line is the single logistic regression model based on the empirical data. Note that the left end of the line does not extend to the baseline; in the absence of any colour differences, three out of 10 eggs were still rejected, because they differed in speckling.

was clearly most important. Rather, differences in spot colour, size, density and cap aggregation were correlated with each other. Replacing spot density with spot size in the best model, for instance, yielded a model with only a slightly worse fit. Among univariate tests of speckling variables, spot density best predicted egg rejection (logistic regression:  $P = 0.019$ ,  $N = 71$ ,  $Sns = 0.47$ ,  $Spc = 0.61$ ,  $R = 0.03$ ; Fig. 2), yet was far inferior to the multivariate speckling model. Therefore, although the birds were assessing differences in speckling, they may have been using a combination of related factors. In addition, the birds were not responding to differences merely in presence or absence of speckles; in fact, 10% more eggs were rejected when host and experimental eggs were the same in this respect than when different.

### Mode of Egg Recognition

In no case did the female reject only her own egg, although in 13 cases out of 96 a host egg was rejected along with the foreign egg. The proportion of nests in which eggs were rejected was virtually the same in one-egg nests (54.3%,  $N = 35$  nests) as in two-egg nests (54.5%,  $N = 55$  nests). This demonstrates that no direct comparison between own and foreign eggs need be performed in



**Figure 2.** Weaverbird rejection of experimental eggs by the difference in spot density between host and experimental eggs. The line is the single logistic regression model based on the empirical data.

order for a weaver to distinguish a foreign egg as such. In fact, the opportunity to make such a comparison does not aid the birds at all in this respect.

## DISCUSSION

Foreign eggs that were dissimilar from the host's own eggs were rejected from West African village weaverbird nests. This suggests that egg rejection behaviour acts as an offspring recognition mechanism in this species, and is concordant with the results from the captive birds studied by Victoria (1972) and with the assumption of Cruz & Wiley (1989) and Robert & Sorci (1999). Village weavers rejected foreign eggs in proportion to the difference in appearance between the foreign and host eggs.

Colour and speckling provided signature information for egg discrimination, but shape and mass did not; this accords with expectations based on the variables' relative reliability. Colour difference was a better predictor of egg rejection than speckling differences, although the birds clearly used both types of information, and used them independently. Moreover, as Rothstein (1982) showed with American robins, *Turdus migratorius*, foreign eggs were more likely to be rejected when both colour and speckling differed, than when only one of these parameters differed. The use of four different variables to assess speckling provided a more precise measure of egg rejection than a single variable estimate. For instance, when we used merely the presence or absence of spots as our criterion for difference in speckling, we found no correlation with rejection rate. However, as the four variables tended to correlate with each other, the statistical prominence of the interaction between spot density and cap aggregation over other factors must be interpreted with caution. Further experiments with painted eggs where certain speckling parameters are kept constant and others varied might be useful in distinguishing their relative importance.

The question of how nonmimetic an egg has to be for it to be rejected, can be addressed first by emphasizing that no sharp threshold over which eggs were rejected was evident in our study population. Rather, the data were consistent with a model where differences in colour and speckling have a graduated and cumulative effect on rejection probability. For instance, an egg that differs in an additional shade of colour will have an additional 55% probability of being rejected. Terms such as 'mimetic' and 'nonmimetic' therefore have limited usefulness in this context. As our results were based on one test per individual, we cannot determine whether the shape of the population response also characterizes individuals. The population-level gradient in parental response as a function of egg appearance differences may correspond to an equally graded response for each individual. However, we cannot exclude the possibility that for each individual weaverbird there is a particular threshold over which eggs are rejected, and that differences in this threshold among individuals have produced the gradient in response at the population level. A study involving a variety of tests per individual would be needed to distinguish these possibilities.

The cognitive (Wright 1992) question of whether village weavers know their own eggs can be answered in the context of three mechanisms by which birds might recognize their eggs, which are not necessarily mutually exclusive: (1) discordancy; (2) direct comparison; or (3) memory alone. This study, like Victoria's (1972) study with this species and Rothstein's (1975) study with catbirds, isolates the third alternative and suggests that female village weaverbirds have a remarkably precise memory for the colour and spotting pattern of their own eggs. Even when presented with the opportunity to compare their own and foreign eggs directly, the females are no better at egg discrimination, suggesting that the second mechanism is not being used at all. This precise ability is adaptive in this species relative to the other two alternatives because of the small clutch size. Rejection by discordancy is a futile strategy for a bird with only two eggs in an average clutch. Recognition by direct comparison is better, but is still suboptimal despite the rarity of double parasitism, because up to a third of yearlings, and a lower proportion of adults, lay only a single egg (Victoria 1972). Since the diderick cuckoo removes an egg when parasitizing (Friedmann 1968), some birds, especially young ones, do not have the opportunity for direct comparison when parasitized, because the parasitic egg is the only one in the nest.

The precision of the village weaverbird's egg discrimination ability is consistent with the hypothesis that interclutch egg variability in weavers is an adaptation for brood parasitism avoidance (Bates 1911). Although this explanation has additional support (Cruz & Wiley 1989), a thorough critical test of this hypothesis would require further research, such as a determination of whether rare egg morphs in the population achieve greater reproductive success because of the parent's ability to reject more parasitic eggs. Other explanations have been offered for this variability. Swynnerton (1916) suggested that village weavers mimic neighbouring species whose eggs are toxic

to predators (Batesian mimicry). We have not found any study documenting natural egg toxicity in a bird. Moreover, each village weaver colony shows a similarly broad range of colour variation (Din 1992; unpublished data); this lack of geographical variation in egg colour is not consistent with a hypothesis of neighbour mimicry. Another alternative is that since predator-mediated selection on egg colour is unlikely in this species (village weaver nests being enclosed), selective restrictions on egg colour have been lifted and genetic drift has resulted in high variability in egg appearance (Moreau 1960). If this is the case, whether a female accepts an introduced egg for incubation should be independent of the difference in appearance between it and her own eggs. We found, on the contrary, that foreign eggs were rejected from West African village weaver nests in proportion to the difference in colour and speckling between the foreign eggs and the host eggs. Egg appearance in this species may have been permitted to diverge by a relaxation of predator-mediated selection for egg crypsis; however, our finding contradicts the hypothesis that this relaxation of selection is sufficient as an explanation for village weaver egg variability.

The broad range of interclutch variability in egg appearance in this species, combined with a precise egg discrimination ability, is consistent with an evolution of these traits in the context of either interspecific brood parasitism by a species that can mimic eggs (as the diderik cuckoo does, Payne 1967) or conspecific brood parasitism (as occurs in a close relative, Jackson 1992), or both.

### Acknowledgments

We thank R. B. Payne for continual indispensable discussions and guidance. For helpful conversations we thank Beverly Rathcke and Christopher Jameson, and also R. D. Alexander, Brian Hazlett and Peter Railton. Comments from Arnon Lotem, Judy Stamps, Sal Cerchio and Laura Payne greatly improved the manuscript. For transportation, advice, and introducing us to The Gambia we are indebted to Clive Barlow. We are grateful to Mansa Dampha for valuable research assistance; to our boatmen Amadou 'Brusan' Jawo and Abraham Jallo, and driver Omar Ndow; and to the rest of the staff at the Bird Safari Camp in Georgetown for their hospitality and friendliness. This project was undertaken by the authority of the Department of Parks and Wildlife in The Gambia, and for this we thank Dr A. Camara, Director; we also thank Research and Development Officer Linda Barnett for her cooperation. The research was partially funded by the Rackham School for Graduate Studies and the Department of Biology at the University of Michigan, and by the National Academy of Sciences of the United States under the administration of Sigma Xi, the Scientific Research Society. The research presented here was evaluated and approved by the Institutional Animal Care and Use Committee of the University of Michigan (Protocol No. 7506) and by the Animal Behavior Society's Animal Care Committee.

### References

- Barlow, C., Wachter, T. & Disley, T. 1997. *A Field Guide to the Birds of The Gambia and Senegal*. Mountfield: Pica Books.
- Bates, G. L. 1911. Further notes on the birds of southern Cameroon. *Ibis*, **5**, 479–545, 581–631.
- Beecher, M. D. 1991. Successes and failures of parent-offspring recognition in animals. In: *Kin Recognition* (Ed. by P. G. Hepper), pp. 94–124. New York: Cambridge University Press.
- Brooke, M. de L., Davies, N. B. & Noble, D. G. 1998. Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. *Proceedings of the Royal Society of London, Series B*, **265**, 1277–1282.
- Colebrook-Robjent, J. F. R. 1984. The breeding of the didric cuckoo *Chrysococcyx caprius* in Zambia. In: *Proceedings of the Fifth Pan-African Ornithological Congress (1980)* (Ed. by J. Ledger), pp. 763–777. Johannesburg: South African Ornithological Society.
- Collias, E. C. 1993. Inheritance of egg-color polymorphism in the village weaver (*Ploceus cucullatus*). *Auk*, **110**, 683–692.
- Collias, N. E. 1984. Egg measurements and coloration throughout life in the village weaverbird, *Ploceus cucullatus*. In: *Proceedings of the Fifth Pan-African Ornithological Congress (1980)* (Ed. by J. Ledger), pp. 461–475. Johannesburg: South African Ornithological Society.
- Collias, N. E. & Collias, E. C. 1970. The behavior of the West African village weaverbird. *Ibis*, **112**, 457–480.
- Cruz, A. & Wiley, J. W. 1989. The decline of an adaptation in the absence of a presumed selection pressure. *Evolution*, **43**, 55–62.
- Da Camara-Smeets, M. 1982. Nesting of the village weaver *Ploceus cucullatus*. *Ibis*, **124**, 241–251.
- Daniel, J. C., Jr. 1957. An embryological comparison of the domestic fowl and the red-winged blackbird. *Auk*, **74**, 340–358.
- Davies, N. B. 2000. *Cuckoos, Cowbirds and Other Cheats*. London: T. & A. D. Poyser.
- Davies, N. B. & Brooke, M. de L. 1989. An experimental study of co-evolution between the cuckoo *Cuculus canorus*, and its hosts. I. Host egg discrimination. *Journal of Animal Ecology*, **58**, 207–224.
- Davies, N. B., Hatchwell, B. J., Robson, T. & Burke, T. 1992. Paternity and parental effort in dunnocks *Prunella modularis*: how good are male chick-feeding rules? *Animal Behaviour*, **43**, 729–745.
- Din, N. A. 1992. Hatching synchronization and polymorphism in the eggs of *Ploceus cucullatus* and *P. nigerrimus* with data on nest parasitism. *African Journal of Ecology*, **30**, 252–260.
- Freeman, S. 1988. Egg variability and conspecific nest parasitism in the *Ploceus* weaverbirds. *Ostrich*, **59**, 49–53.
- Friedmann, H. 1968. The evolutionary history of the avian genus *Chrysococcyx*. *U.S. Museum of Natural History Bulletin*, **265**, 1–137.
- Hosmer, D. W., Jr & Lemeshow, S. 1989. *Applied Logistic Regression*. New York: J. Wiley.
- Hunter, H. C. 1961. Parasitism of the masked weaver *Ploceus velatus arundinaceus*. *Ostrich*, **32**, 55–63.
- Jackson, W. M. 1992. Relative importance of parasitism by *Chrysococcyx* cuckoos versus conspecific nest parasitism in the northern masked weaver *Ploceus taeniopterus*. *Ornis Scandinavica*, **23**, 203–206.
- Jackson, W. M. 1998. Egg discrimination and egg-color variability in the northern masked weaver: the importance of conspecific versus interspecific parasitism. In: *Parasitic Birds and Their Hosts: Studies in Coevolution* (Ed. by S. I. Rothstein & S. K. Robinson), pp. 407–418. New York: Oxford University Press.
- Jensen, R. A. C. & Vernon, C. J. 1970. On the biology of the didric cuckoo in southern Africa. *Ostrich*, **41**, 237–246.

- Lahti, D. C.** In press. A case study of assessment and prediction in invasion biology: the village weaverbird *Ploceus cucullatus*. *Animal Biodiversity and Conservation*.
- Lahti, D. C., Lahti, A. R. & Dampah, M.** In press. Associations between nesting village weavers *Ploceus cucullatus* and other animal species in The Gambia. *Ostrich*, **73**.
- Lawes, M. J. & Kirkman, S.** 1996. Egg recognition and interspecific brood parasitism rates in red bishops (Aves: Ploceidae). *Animal Behaviour*, **52**, 553–563.
- Lindholm, A. K. & Thomas, R. J.** 2000. Differences between populations of reed warblers in defences against brood parasitism. *Behaviour*, **137**, 25–42.
- Lotem, A., Nakamura, H. & Zahavi, A.** 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. *Behavioral Ecology*, **3**, 128–132.
- Lotem, A., Nakamura, H. & Zahavi, A.** 1995. Constraints on egg discrimination and cuckoo host coevolution. *Animal Behaviour*, **49**, 1185–1209.
- Macleay, G. L.** 1993. *Roberts' Birds of Southern Africa*. Cape Town, South Africa: Trustees of John Voelcker Bird Book Fund.
- Mittlböck, M. & Schemper, M.** 1999. Computing measures of explained variation for logistic regression models. *Computer Methods and Programs in Biomedicine*, **58**, 17–24.
- Moksnes, A.** 1992. Egg recognition in chaffinches and bramblings. *Animal Behaviour*, **44**, 993–995.
- Moreau, R. E.** 1960. Conspectus and classification of the ploceine weaver-birds. *Ibis*, **102**, 298–321, 443–471.
- Morel, G. & Morel, M.-Y.** 1962. La reproduction des oiseaux dans une région semi-aride: la Vallée du Sénégal. *Alauda*, **30**, 161–203.
- Nakamura, H., Kubota, S. & Suzuki, R.** 1998. Coevolution between the common cuckoo and its major hosts in Japan. In: *Parasitic Birds and Their Hosts: Studies in Coevolution* (Ed. by S. I. Rothstein & S. K. Robinson), pp. 94–112. New York: Oxford University Press.
- Payne, R. B.** 1967. Interspecific communication signals in parasitic birds. *American Naturalist*, **101**, 363–375.
- Payne, R. B.** 1997. Avian brood parasitism. In: *Host-Parasite Evolution: General Principles and Avian Models* (Ed. by D. H. Clayton & J. Moore), pp. 338–369. Oxford: Oxford University Press.
- Peeters, E. T. H. M. & Gardeniers, J. J. P.** 1998. Logistic regression as a tool for defining habitat requirements of two common gammarids. *Freshwater Biology*, **39**, 605–615.
- Reed, R. A.** 1968. Studies of the diederik cuckoo *Chrysococcyx caprius* in the Transvaal. *Ibis*, **110**, 321–331.
- Robert, M. & Sorci, G.** 1999. Rapid increase of host defence against brood parasites in a recently parasitized area: the case of village weavers in Hispaniola. *Proceedings of the Royal Society of London, Series B*, **266**, 1–6.
- Romanoff, A. L.** 1960. *The Avian Embryo: Structural and Functional Development*. New York: Macmillan.
- Rothstein, S. I.** 1975. Mechanisms of avian egg-recognition: do birds know their own eggs? *Animal Behaviour*, **23**, 268–278.
- Rothstein, S. I.** 1982. Mechanisms of avian egg recognition: which egg parameters elicit responses by rejector species? *Behavioral Ecology and Sociobiology*, **11**, 229–239.
- Schönwetter, M.** 1983. Familie Ploceidae. In: *Handbuch der Oologie* (Ed. by W. Meise), pp. 513–576. Berlin: Akademie-Verlag.
- Soler, J. J. & Møller, A. P.** 1996. A comparative analysis of the evolution of variation in appearance of eggs of European passerines in relation to brood parasitism. *Behavioral Ecology*, **7**, 89–94.
- Soler, J. J., Martinez, J. G., Soler, M. & Møller, A. P.** 1999. Genetic and geographic variation in rejection behavior of cuckoo eggs by European magpie populations: an experimental test of rejecter-gene flow. *Evolution*, **53**, 947–956.
- Stokke, B. G., Moksnes, A., Røskoft, E., Rudolfsen, G. & Honza, M.** 1999. Rejection of artificial cuckoo (*Cuculus canorus*) eggs in relation to variation in egg appearance among reed warblers (*Acrocephalus scirpaceus*). *Proceedings of the Royal Society of London, Series B*, **266**, 1483–1488.
- Swynnerton, C. F. M.** 1916. On the coloration of the mouths and eggs of birds. II. On the coloration of eggs. *Ibis*, **4**, 529–606.
- Victoria, J. K.** 1972. Clutch characteristics and egg discriminative ability of the African village weaverbird *Ploceus cucullatus*. *Ibis*, **114**, 367–376.
- Villalobos-Dominguez, C. & Villalobos, J.** 1947. *Atlas de Los Colores*. Buenos Aires, Argentina: Liberia El Ateneo.
- Wetmore, A. & Swales, B. H.** 1931. The birds of Haiti and the Dominican Republic. *U.S. Museum of Natural History Bulletin*, **155**, 1–459.
- Wright, A. A.** 1992. The study of animal cognitive processes. In: *Cognitive Aspects of Stimulus Control* (Ed. by W. K. Honig & J. G. Fetterman), pp. 225–241. Hillsdale, New Jersey: L. Erlbaum.