

ECOLOGY AND EVOLUTION OF BREEDING ADAPTATIONS IN THE  
VILLAGE WEAVER *PLOCEUS CUCULLATUS*

by

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"One egg is like another."

-Cervantes, *Don Quixote*, part II (1615), bk.III, ch.14.

"'Tis good to keep a nest egg."

-Cervantes, *Don Quixote*, part II (1615), bk.III, ch.7.

(Sometimes the first point raises problems for the second.)

## **DEDICATION**

To four individuals who, through their knowledge and their willingness to share it with me generously and enthusiastically, encouraged my love for nature and showed me that I could make a career out of exploring and seeking to understand it:

(the memory of) Thomas C. Dent, Botanist

David C. Mahan, Aquatic Biologist

Joseph K. Sheldon, Entomologist

Richard T. Wright, Ecologist

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## TABLE OF CONTENTS

<b>Dedication</b>	ii
<b>Acknowledgments</b>	iii
<b>List of Tables</b>	viii
<b>List of Figures</b>	ix
<b>Chapter 1. Introduction</b>	1
Species Introductions and Natural Selection	1
Introductions of the Village Weaver <i>Ploceus cucullatus</i>	4
Brood Parasite – Host Interactions as a Model System for the Study of Natural Selection	4
Case Study: Defenses Against Brood Parasitism in the Village Weaver	5
Structure of the Dissertation	10
References	14
<b>PART I. A CONTRIBUTION TO VARIOUS ASPECTS OF THE BREEDING ECOLOGY OF THE VILLAGE WEAVER</b>	20
<b>Chapter 2. Associations between Nesting Village Weavers <i>Ploceus cucullatus</i> and Other Animal Species in The Gambia</b>	21
References	27
<b>Chapter 3. Cactus Fruits May Facilitate Village Weaver (<i>Ploceus cucullatus</i>) Breeding in Atypical Habitat on Hispaniola</b>	29
References	36

<b>Chapter 4.</b>	<b>A Case Study of Species Assessment in Invasion Biology: The Village Weaverbird <i>Ploceus cucullatus</i></b>	39
	Regions of Past and Possible Future Naturalization	41
	Factors Influencing Introduction and Invasion Success	45
	Agricultural Pest Status	51
	Smallwood-Salmon Rating System	53
	Suggestions for Prevention and Control	54
	References	60
<b>PART II.</b>	<b>THE EVOLUTION OF DEFENSES AGAINST BROOD PARASITISM IN THE VILLAGE WEAVER</b>	69
<b>Chapter 5.</b>	<b>How Precise is Egg Discrimination in Weaverbirds?</b>	70
	Introduction	71
	Methods	75
	Results	80
	Discussion	83
	References	92
<b>Chapter 6.</b>	<b>Evolution of Egg Appearance Following a Change in Selective Regime</b>	98
	Introduction	98
	Methods	104
	Results	109
	Discussion	114
	References	152

<b>Chapter 7.</b>	<b>Does Egg Recognition Decay in the Absence of Cuckoo Brood Parasitism?</b>	162
	Introduction	162
	Methods	167
	Results	172
	Discussion	178
	References	202
<b>Appendix.</b>	<b>Eigenvectors for Principal Component Analysis of Differences Between Host and Experimental Eggs</b>	209

## LIST OF TABLES

### Table

1.1	Necessary Criteria for Effective Evolutionary Analysis of Change in a Heritable Trait by Comparison of Source and Introduced Populations	3
1.2	Hypotheses Tested in Part II of This Dissertation	7
4.1	Factors Correlated with Introduction Success and Invasiveness in Birds, and Relation to the Village Weaver <i>Ploceus cucullatus</i> (VW)	56
4.2	Expected Ratings of Concern for Invasion, According to the Smallwood-Salmon Rating System (Smallwood & Salmon 1992)	59
5.1	Quantification of Egg Speckling Variables by Indexing	88
5.2	Parameters of Multiple Logistic Regression Model, Predicting Egg Rejection on the Basis of Egg Colour and Speckling Differences Between Host and Foreign Eggs	89
6.1	Sources of Variation in Egg Appearance in the Village Weaver	133
6.2	Comparison of Within-Clutch Variation in Egg Spotting Among Populations of the Village Weaver	134
7.1	Foreign Egg Rejection on the Basis of Egg and Clutch Characteristics: Four-Population Combined Logistic Regression Model	191
7.2	Foreign Egg Rejection on the Basis of Egg and Clutch Characteristics: Single-Population Logistic Regression Models	192
7.3	Egg Rejection by Village Weavers in the Dominican Republic: Replication of Cruz & Wiley (1989)	193
7.4	Egg Rejection by Village Weavers in the Dominican Republic: Replication of Robert & Sorci (1999)	194

## LIST OF FIGURES

Figure		
3.1	Ripe Fruit of <i>Stenocereus hystrix</i> in the Dominican Republic, Having Been Fed Upon by Village Weavers	35
5.1	Weaver Rejection of Experimental Eggs by the Difference in Colour Between Host and Experimental Eggs	90
5.2	Weaver Rejection of Experimental Eggs by the Difference in Spot Density Between Host and Experimental Eggs	91
6.1	Geographic Range of the Village Weaver ( <i>Ploceus cucullatus</i> ).	135
6.2	Fourteen Complete Clutches (a-n) of Village Weaver ( <i>Ploceus cucullatus</i> ) Eggs, from Janjangbureh Island, The Gambia (Actual Size)	136
6.3	Spectra of 18 Eggs in Different Clutches of the Village Weaver, Dominican Republic (all eggs scored as E 12/6, a medium blue-green, on <i>Villalobos Color Atlas</i> (Villalobos 1947))	137
6.4	Spectra of a 4-Egg Clutch of a Village Weaver, South Africa (all eggs scored as E 19/0, white, on <i>Villalobos Color Atlas</i> (Villalobos 1947))	138
6.5	Spot Size in Village Weaver Eggs: Relation of Quantitative Measurements to Index Categories (means above each column)	139
6.6	Spot Density in Village Weaver Eggs: Relation of Quantitative Measurements to Index Categories (means above each column)	140
6.7	Spot Color in Village Weaver Eggs: Relation of Quantitative Measurements to Index Categories	141
6.8	Spot Aggregation in Village Weaver Eggs: Relation of Quantitative Measurements to Index Categories (means above each column)	142

6.9	ANOVAs of Within-Clutch Disparity in (A) Egg Shape and (B) Egg Mass Between Village Weaver Populations	143
6.10	ANOVAs of Between-Individual Disparity in (A) Egg Shape and (B) Egg Mass Between Village Weaver Populations	144
6.11	ANOVAs of Within-Clutch Disparity in (A) Egg Brightness and (B) Egg Chroma Between Village Weaver Populations	145
6.12	ANOVAs of Between-Individual Disparity in Egg Brightness Between Village Weaver Populations, by (A) Color Charts, and (B) Spectrophotometry	146
6.13	ANOVAs of Between-Individual Disparity in Eggshell Chroma Between Village Weaver Populations, by (A) Color Charts, and (B, C) Spectrophotometry	147
6.14	Population-Level Egg Color Variability in Village Weavers: South Africa vs. Mauritius	148
6.15	Population-Level Egg Color Variability in Village Weavers: The Gambia vs. Dominican Republic	149
6.16	Variation in Egg Color Within and Between Village Weaver Nest Aggregations in The Gambia	150
6.17	Hypothesized Impact on Embryo Fitness of Different Colors of Eggs in Different Light Environments	151
7.1	Graphical model of the Relationship Between Egg Variability and Egg Rejection Behavior	195
7.2	Match of Paint to Actual Village Weaver Egg Colors (Spectra): (A) dark blue-green (control), (B) off-white	197
7.3	Relationship of (A) PC1 and (B) PC3 Values to Sample Spectral Differences Between Host and Experimental Eggs	198
7.4	Village Weaver Rejection of Eggs by Difference in Color Host and Experimental Eggs: Logistic Regression Model	199
7.5	Village Weaver Rejection of Eggs by Difference in Color Host and Experimental Eggs: Plot of Acceptances and Rejections in Color Difference Space	200

7.6	Village Weaver Rejection of Eggs by Difference in Spot Density Between Host and Experimental Eggs	201
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## ABSTRACT

### ECOLOGY AND EVOLUTION OF BREEDING ADAPTATIONS IN THE VILLAGE WEAVER *PLOCEUS CUCULLATUS*

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Chair: Robert B. Payne

Introduced species can provide rare opportunities to test hypotheses of adaptation and evolution by natural selection. The main part of this dissertation is a test of predictions from two hypotheses regarding the evolution of traits in a colony-nesting African passerine bird, the village weaver (Aves: Ploceidae): (1) Egg appearance characteristics and egg rejection behavior function to direct parental care to offspring; and (2) these traits are maintained by natural selection primarily as counteradaptations to brood parasitism by the egg-mimicking diederik cuckoo *Chrysococcyx caprius*. Predictions from these hypotheses were met by observations and egg-replacement experiments in four populations (The Gambia, South Africa, Mauritius, and Dominican Republic) between 1999 and 2001.

A comparative study between two natural weaver populations in sympatry with the diederik cuckoo, and two introduced populations that have been in allopatry with the diederik cuckoo for 115 and >200 years respectively, demonstrates a decline in anti-parasite adaptations in the absence of the cuckoo. Within-clutch variability in egg color and spotting increased, and between-individual variability decreased. Decay of these traits correlated with duration of divergence from the respective source populations. The efficiency of egg rejection behavior also declined, but solely as a byproduct of the

evolution of egg appearance characteristics; no decline in the perceptual or cognitive basis for egg recognition occurred.

A general hypothesis based on solar damage to embryonic viability may explain observed directional evolution of egg color in introduced village weavers, as well as the blue to blue-green color of many arboreal birds' eggs. A graphical model explains the interaction between egg recognition and egg variability in brood parasite - host systems. The evolution of the latter but not the former in the present study is explained by the hypothesis that nonfunctional morphological traits may generally be more subject to direct selection than nonfunctional behavioral traits are.

This work contributes to our understanding of (1) coevolution or reciprocal adaptation between brood parasites and their hosts; (2) natural selection and evolution in natural populations over brief time spans; and (3) the dynamics of trait decay.

## **CHAPTER 1**

### **INTRODUCTION**

Observations described throughout the biological literature provide overwhelming evidence that organisms tend to be well suited to their environments, attesting to the role of natural selection in the evolutionary process. Nevertheless, the action of natural selection in specific cases is difficult to infer for several reasons, among them methodological constraints and the fact that relevant traits are often fixed, the changes responsible for them having occurred in the inaccessible past. According to Endler (1986), there are only two ways to detect natural selection that permit the inference of a cause-effect relationship between environment and trait: observing correlations of environmental factors with trait values, or perturbing a population's environment and observing a trait change. The main part of this dissertation is a test of the action of natural selection by the second of these methods. The environmental perturbation in this case is human introduction of the focal species into an environment that differs from that of the source population.

#### **Species Introductions and Natural Selection**

One of the best situations for a study of short term evolutionary change is the establishment of an introduced population in an area where the selective regime with regard to a particular trait or suite of traits is significantly different from that of the source population (Thompson 1998). This approach is exemplified by work on the house sparrow *Passer domesticus* introduced into the Americas (Johnston & Selander 1964);

more recently, short term evolutionary change in morphology has been documented in introduced *Anolis* lizards (Losos et al. 1997) and *Spartina* cordgrass (Daehler & Strong 1997). Behavioral divergence has been documented for *Baetis* mayflies (Flecker 1992) and *Poecilia* guppies (Magurran et al. 1992).

Writers have emphasized various guidelines relevant to the inference of natural selection (Endler 1986; Alcock 1993; Futuyma 1998). Applying these guidelines particularly to the comparative study of traits in source and introduced populations of a species, a number of necessary conditions emerge for rigorous tests (Table 1.1). Besides the issue of heritability, one must choose a measurable trait that is known to have a strong influence on survival or reproduction. The two environments must be different enough and uniform enough to produce clearly different selective regimes on the trait in question. Variation in the trait within any one population must be low enough to permit resolution of differences between populations. Problems such as later introductions or immigration which undermine reproductive isolation between the populations, and environmental changes which affect the selective regime on either population, can easily compromise the experimental conditions. Historical information must be available regarding the time period of the introduction and the identity of the source population, and the divergence must have taken place long enough ago to permit the presumed selection differential to have a detectable effect. A study should also consider the possibility that observed differences are due to either genetic drift, or a founder effect (Mayr 1963) where genetic diversity of the introduced population was originally low and the trait values have been biased by chance. In cases where a species has been successfully introduced to more than one location, these replicates may at least partially deal with such possibilities, in addition to the other advantages of multiple tests over a single test.

If the trait in question possesses a degree of adaptive plasticity that can account for geographic variation in expression without the differential action of natural selection,

a simple comparison of traits across populations will not be sufficient to establish that evolution has occurred. With adaptive plasticity it is possible that the environments of the two populations produce cues which the individuals use to express a trait differently. In these cases there will be value in reproducing relevant aspects of the parental environment in the introduced population, thereby controlling for differences in cues. Such experimental induction is very difficult to achieve in most cases, often because the relevant cues can only be surmised, or because they cannot be faithfully reproduced. Flecker's (1992) removal of introduced fish from a stream to simulate an ancestral state is an instance of such experimental induction. If the experiment begins after individuals could have had some experience, such as imprinting, that set them on an environment-specific ontogenetic trajectory, trait differences caused by genetic differences cannot be distinguished from developmental plasticity.

<i>Trait Conditions</i>	<i>Historical Conditions</i>	<i>Ecological Conditions</i>
1. The trait is quantifiable and amenable to experimentation.	4. The identity of the source population is known.	7. Gene flow between the populations is negligible.
2. The status of the trait differs between populations, and any cues modulating its expression in the source population can be experimentally reproduced in the introduced population.	5. The time period of the introduction is known, and occurred long enough ago for trait divergence to have taken place.	8. The environments of the two populations provide significantly different selective regimes on the trait.
3. There is low variation in the trait in each population relative to the expected difference between populations.	6. A replicate, or some other means, is available to address the possible role of a founder effect or genetic drift.	9. Changes since introduction in the selective regime on the trait in each population are absent, or at least simple and tractable.

**Table 1.1. Necessary Criteria for Effective Evolutionary Analysis of Change in a Heritable Trait by Comparison of Source and Introduced Populations**

Insofar as the conditions outlined in Table 1.1 are met, hypotheses of response to natural selection may be tested, by determining whether the trait in question differs in the two populations in accordance with the difference in the respective selective regimes.

### **Introductions of the Village Weaver *Ploceus cucullatus***

The research described in this dissertation takes advantage of the introduction history of a common sub-Saharan African passerine bird, the village weaver (*Ploceus cucullatus*) (see chapter 4). Evidence indicates that the West African form of this species, *P.c.cucullatus*, was successfully introduced from the West African region of Senegambia to the Caribbean island of Hispaniola over two hundred years ago, probably involving a series of introductions over several decades. A southern African bird is allopatric with *P.c.cucullatus* in Africa, is similar to it in most morphological respects except for certain plumage characteristics, and is usually considered along with several other forms in other areas of Africa to be conspecific (*P.c.spilonotus*). This form was introduced to the Mascarene island of Mauritius in 1886, and records indicate no further introductions to that island. The village weaver in both introduced populations is presently abundant, and experiences no known gene flow with the parental populations in Africa.

### **Brood Parasite – Host Interactions as a Model System for the Study of Natural Selection**

Brood parasitism in birds occurs when females lay eggs in nests of other birds, thereby transferring the costs of parental care to the host (Payne 1977, 1997; Davies 2000). The brood parasite-host relationship provides a model system for the study of the action of natural selection, and particularly reciprocal adaptation (Davies & Brooke 1988; Rothstein 1990). Rothstein (1990) mentions several features of brood parasitism

that facilitate such study: (1) Most hosts are parasitized by a single species, which simplifies the estimation of reciprocal fitness effects. (2) Parental care in birds is elicited by the same sensory modalities (vocal and visual cues) that humans stress. (3) Nearly all of the major adaptations related to parasite-host interactions are manifested in or near the nest. (4) A brood parasite's fitness typically is maximized when its egg replaces the host's entire brood. The action of natural selection in the context of brood parasitism depends strongly on the impact of the interaction on the fitness of the participants, and this impact varies in the several phylogenetic incidences of obligate interspecific brood parasitism. For example, the impact of an instance of brood parasitism on a host's fitness is generally greater when the parasite is a *Cuculus* cuckoo rather than a *Molothrus* cowbird, and a cowbird has more impact than a *Vidua* finch (Payne 1997).

Experimental studies have provided an understanding of the evolution of the relationships of brood parasites and their hosts (Rothstein 1975; Davies & Brooke 1989; Payne et al. 1998, 2000, 2001). Despite the promise of such systems for demonstrating the action of natural selection over time in particular cases, existing studies show how difficult gathering the appropriate data can be, and how rare the conditions are that facilitate such studies (see review in Payne 1997: 355).

### **Case Study: Defenses Against Brood Parasitism in the Village Weaver**

In Africa the diderik cuckoo *Chrysococcyx caprius* is a brood parasite of the village weaver, among other species (Morel & Morel 1962; Payne in press). Throughout its native range the village weaver is an abundant and frequently parasitized host of the diderik cuckoo. The cuckoo nestlings generally hatch early and remove any host eggs from the nest (Payne 1967, 1977). The host proceeds to raise the parasite to fledging. Unlike the situation in cowbird parasitism, most of the cost of cuckoo parasitism to the host occurs after the parasitic egg has been laid in the nest, due to host egg ejection by

the cuckoo chick (Payne 1997). A parasitized cuckoo host therefore has an opportunity, at least theoretically, to avert a large portion of the fitness costs associated with parasitism.

Diederik cuckoo eggs look very similar to weaver eggs, and appear to have evolved to mimic them in appearance (Chapin 1954; Jensen & Vernon 1970; Payne in press). After the parasitic egg is laid, the conflict of interests between cuckoo and weaver becomes focused on the information provided by egg appearance. The cuckoo has an interest in counterfeiting a weaver egg, the weaver in detecting the forgery. As with other challenges to identity recognition in nature, signature information (Beecher 1991) may be expected to evolve in weaver eggs. A signature is a signal that functions in recognition of identity by being consistent within an individual (or group, depending on what requires identification), and being distinctive within the broader population. In the case of egg appearance, a signature would be a projection or extension of the maternal phenotype (in the sense of Dawkins 1982), since neither the individual in the egg nor its father has any influence on egg appearance in birds (Lang & Wells 1987; Collias 1993). The signature in this case can still be considered a communicative signal. The sender and receiver of the signal are the same individual; the host is communicating with herself.

Some evidence exists that village weavers do exhibit signature information with their eggs, although a recent review has called for more work on this subject (Underwood & Sealy 2002). Village weaver females lay eggs that are highly variable in appearance between individual females, and consistent within an individual throughout her lifetime (Collias 1984). Moreau (1964) claimed that egg variability at the local population or species level was probably higher in the *Ploceus* weavers than in any other group of birds (see also Schönwetter 1983; Freeman 1988). Bates (1911) first suggested that such egg variability would allow a village weaver to distinguish her eggs from foreign eggs. Although both egg variability and its relationship with egg discrimination have only now

been assessed (see chapters 5-7), Victoria (1972) showed in a captive population that village weavers do recognize their own eggs and practice egg rejection.

Given village weaver egg variability and the impact on village weaver fitness of a failure to detect a cuckoo egg as foreign and respond to it appropriately, several hypotheses follow (Table 1.2).

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***H1:*** Egg recognition and rejection in the village weaver function to direct parental care to offspring.

---

***H2:*** Egg appearance characteristics function as maternal signatures for indirect recognition of offspring.

---

***H3:*** Egg recognition and rejection in the village weaver are maintained by natural selection primarily as counteradaptations to interspecific brood parasitism.

---

***H4:*** Low intraclutch variability and high interindividual variability in egg appearance in the village weaver are maintained by natural selection primarily as counteradaptations to interspecific brood parasitism.

---

**Table 1.2. Hypotheses Tested in Part II of This Dissertation**

The main part of this dissertation is an attempt to test these hypotheses in two ways: by experimentally testing the functional claims the hypotheses make about the traits involved; and by performing a comparative analysis among populations to test whether the traits in question decline in the absence of selection pressure in a relatively short period of time (100-200 years).

Village weavers in Africa have evolved in the context of brood parasitism by the diederik cuckoo, presumably for thousands of years. The introduced populations of this

species on the islands of Mauritius and Hispaniola, however, have been released from the selection the cuckoo exerted on their ancestors; there are no diederik cuckoos or other egg-mimicking brood parasites on either island. Village weavers are not known to engage in intraspecific parasitism, although such has been documented in other *Ploceus* species (Freeman 1988; Jackson 1992).

Egg rejection behavior is expected to be adaptive in the presence of brood parasitism, but not in its absence, when egg-ejecting cuckoos are the parasites (Davies & Brooke 1989). Evolutionary theory predicts that in a population where there is no danger of cuckoo parasitism, the village weaver should eventually lose the ability to discriminate eggs and reject dissimilar ones. This decline would be hastened if weavers reject their own unusual eggs.

Cruz and Wiley (1989) suggested that egg rejection behavior had declined in the introduced Hispaniolan population relative to the presumed African level (based on data from Victoria (1972)), due to the absence of selection pressure by cuckoos. Subsequently, Robert and Sorci (1999) reported what they considered to be a higher egg rejection rate in the Hispaniolan population, and attributed the difference between their results and those of Cruz and Wiley (1989) to a recent colonization of the weavers by the brood parasitic shiny cowbird *Molothrus bonariensis*. However, neither of these studies quantified egg appearance differences or modeled egg rejection as a function of egg appearance, and their varying methods do not permit comparison of relative rates among studies. For instance, as chapter 5 illustrates, rejection rates of anywhere from 0 to 100% can be achieved depending on the precise color and spotting pattern differences that exist between experimental and host eggs. In order to compare rates of rejection in introduced and parental populations, identical methods must be employed in both locations, and the relationship between egg rejection and difference in appearance between own and foreign eggs must be compared between populations. Moreover, the shiny cowbird lays eggs that are very different in appearance from those of the Hispaniolan village weaver. Refined

egg discrimination is not required for the rejection of cowbird eggs, and the experimental use of cowbird eggs does not address the question of whether a population has declined in ability to avoid parasitism by an egg-mimicking cuckoo. Nevertheless, the studies of Cruz and Wiley (1989) and Robert and Sorci (1998) do raise the possibility that hosts of brood parasites that have been removed from parasitism in the historical past may change in their ability to discriminate their own from foreign eggs.

If natural selection maintains egg appearance characteristics that village weavers use to discriminate own from foreign eggs, then the reliability of these characteristics, including consistency within a clutch and distinctiveness within the population, may also be expected to decline after the source of selection is removed. As has been proposed for egg rejection behavior, a tradeoff may be involved such that loss of these clutch characteristics is adaptive in the absence of cuckoo brood parasitism. For instance, distinctiveness of egg appearance within the population might require the production of pigment concentrations or combinations that bear some physiological cost relative to pigment production in an individual from an historically unparasitized population. The maintenance of similarity within a clutch, likewise, could involve costly precision in the application of pigment from egg to egg, analogous to the precision that is thought to be required for bodily symmetry (Møller & Thornhill 1998). No study has yet assessed costs of clutch distinctiveness or uniformity. If such costs are negligible, loss of nonfunctional characters is still expected to occur, though at a slower rate, through mutation accumulation (Fong et al. 1995). Unfortunately, our ignorance as to how fast traits decay in the absence of selection pressure reduces the specificity of the predictions that can be made at this point. Detectable decay of traits in the absence of selection has been found in under 100 generations in *Spartina* cordgrass (Daehler & Strong 1997) and *Poecilia* guppies (Magurran et al. 1992).

The village weaver is a candidate of choice for an analysis of adaptive trait change, according to the conditions summarized in Table 1.1. The absence of brood

parasitism by an egg-mimicking cuckoo in the introduced populations is expected to be a significant selective change from the ancestral situation. Egg variability and rejection behavior are quantifiable, and the latter is amenable to experimentation, following an established methodology of experimental brood parasitism (Rothstein 1975; Lawes & Kirkman 1996; Jackson 1998; Stokke et al. 1999; Lindholm & Thomas 2000). An experimenter can simulate the condition of brood parasitism in a nonparasitized population by placing foreign eggs into nests. Models of egg rejection behavior and matrices describing egg variability can then be compared across populations. The source populations of the introductions are known with some precision (Wetmore & Swales 1931; Lever 1987). Two independent introductions have occurred, one into the Mascarene Islands and one into the Caribbean, permitting a test of evolution over two different time periods, and potentially providing insight into the role of founder effects. There are no reports of continuing introductions into either population.

### **Structure of the Dissertation**

This dissertation is composed of two parts. The first is a contribution to various aspects of the breeding ecology of the village weaver, and (after this Introduction) is divided into three chapters.

Chapter 2 summarizes observations of nesting associations between the village weaver and other species in The Gambia, West Africa. The interactions appear to range from parasitic to commensal to mutualistic, although no test of the nature of these relationships has yet been performed. Some of the associations presented in Chapter 2 have not been documented before in weavers.

Chapter 3 discusses an observation of breeding in atypical habitat in Dominican Republic, and proposes a hypothesis to explain it. Breeding is coincident with rainfall in many bird species. In the village weaver, rainfall predicts breeding patterns both temporally and geographically. Documentation in Chapter 3 of breeding in the arid

habitat of northwest Dominican Republic is the first published exception to this rule. Succulent fruits may provide a "rainfall substitute", facilitating breeding in otherwise inhospitable habitat, just as captive populations are kept breeding artificially by provisioning.

Chapter 4 is an application of our knowledge of the breeding biology and other aspects of the natural history of the village weaver to the study of invasive species. Current knowledge, including original field observations, permits an assessment of the concern the village weaver merits due to its opportunism, tendency to successfully establish and spread following introduction into a new habitat, and agricultural pest status. Available information indicates geographical areas of likely future invasion or damage, and recommendations for control and prevention. Between 1999 and 2002, several databases have been analyzed providing correlative evidence that specific factors influence a species' likelihood of establishment or spread in a new area. This case study is the first published assessment of the invasive potential of a species using these analyses.

The second and main part of this dissertation is a study of one general area of the breeding biology of the village weaver: its responses to brood parasitism. This part highlights the related traits of egg rejection behavior and egg appearance characteristics. This work is based on experiments performed in four localities (The Gambia, South Africa, Mauritius, and Dominican Republic) between 1999 and 2001. Together the three chapters test the hypotheses in Table 1.2.

Chapter 5 provides experimental evidence that village weavers in Africa (1) recognize and reject eggs that differ in appearance from their own, and (2) use both color and spotting pattern as cues in egg recognition. Moreover, (3) village weavers remember the appearance of their own eggs, such that they need not have one of them in the nest for comparison at the time of parasitism, in order to recognize a foreign egg. A sigmoid function effectively characterizes the relationship between the difference in color and

spotting of own vs. foreign eggs, and the rate of rejection of foreign eggs. This chapter's results are consistent with the hypothesis that egg recognition and rejection in the village weaver function to direct parental care to one's own offspring (**H1**, Table 1.2), and that egg appearance characteristics function as maternal signatures for indirect offspring recognition (**H2**, Table 1.2).

Chapter 6 assesses egg appearance in the village weaver, from clutches in two parasitized African populations (in South Africa and The Gambia), and an unparasitized population introduced from each of those African populations (Mauritius and Dominican Republic respectively). Quantification of within-clutch and between-individual variation, and comparison among populations, provides evidence that (1) egg color and spotting provide consistent signature information in the parasitized parental populations whereas egg size and shape do not; (2) signature information provided by egg appearance is slightly less reliable in Mauritius than in South Africa which was the source of the Mauritian population over a hundred years ago; and (3) this signature information is much less reliable in the Dominican Republic than in The Gambia which was the source of the Dominican population over 200 years ago. This chapter's results corroborate the conclusions of the last chapter, and provide evidence for the hypothesis that low intraclutch variability and high interindividual variability in egg appearance in the village weaver are maintained by natural selection primarily as counteradaptations to interspecific brood parasitism (**H4**, Table 1.2). These counteradaptations decay in the absence of selection, to a greater extent the longer the population is removed from brood parasitism by a cuckoo with egg mimicry.

Chapter 7 describes an experimental study of egg rejection behavior in the same populations, source and introduced, as in the previous chapter. This chapter corroborates the conclusions of chapter 5, provides evidence of a cost of egg rejection (damage to own eggs), and extends our understanding of the dynamics of egg recognition and rejection behavior. Specifically, (1) village weavers reject eggs according to the difference in color

and spotting characteristics. With regard to color, brightness (average reflectance over all light wavelengths) is especially important. Difference in chroma, or color intensity, is also a predictor of egg rejection, although the particular way in which chroma is used differs among populations. (2) Village weavers tend to reject eggs more after their clutch is completed than during the laying period. (3) Because of the intraclutch egg variability differences among populations (see chapter 6), egg recognition is less efficient in the introduced populations than the source populations. (4) Because of the interindividual egg variability differences among populations (see chapter 6), recognition of eggs from other members of the same population is less efficient in the introduced populations than the source populations. This result is inconsistent with the hypothesis that *intraspecific* (village weaver) parasitism is an important source of selection on egg appearance characteristics and egg rejection behavior, but is consistent with the hypothesis that egg recognition and rejection in the village weaver are maintained by natural selection primarily as counteradaptations to *interspecific* brood parasitism (**H3** and **H4**, Table 1.2). (5) Controlling for differences between populations in egg variability within and between clutches, there is no additional decline in egg rejection behavior in the introduced populations relative to their source populations. The ability to use color and spotting information to determine the difference between own and foreign eggs has remained latent but consistent in populations removed from cuckoo parasitism, despite (i) the decline in the efficiency of the trait due to decreased reliability of egg signatures, and (ii) the decrease in the trait's adaptive value.

Two brief appendices follow chapter 7. Measurement of color has recently become a focus of discussion among ornithologists and other vertebrate zoologists. Appendix I describes the two principal methods of egg color quantification in chapters 5-7, and compares their efficacy: subjective comparisons of eggs with color charts, and quantitative measurement of egg color by UV-VIS spectrophotometry. Appendix II

discusses observed variation in clutch size across populations of the village weaver and proposes a hypothesis to explain it.

The instances in which variation in traits facilitate tests for adaptation and the operation of natural selection are rare. Even in the promising area of comparative studies of introduced vs. source populations there are numerous trait-related, historical, and ecological conditions which compromise the power of evolutionary studies in most cases (Table 1.1). These conditions are met in the village weaver with respect to its responses to brood parasitism. This indicates the high value of this “natural experiment”; it is capable of providing needed insights into the way in which evolution works. In particular, light is shed on how, and how quickly, traits evolve in response to a change in selection differential. This complements the growing body of work of other researchers on the subject of natural selection and rapid evolution (Thompson 1998). Furthermore, brood parasitism is suspected to be a cause of decline in many bird species, and is an area of vigorous research interest partially for this reason (Brittingham & Temple 1983; Askins 1995). A recent review (Rothstein & Robinson 1998) considers the question “Do hosts lose rejection behavior in the absence of parasitism?” to be one of the major unanswered questions in the study of avian brood parasitism. This dissertation directly addresses this question.

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PART I

A CONTRIBUTION TO VARIOUS ASPECTS OF THE BREEDING ECOLOGY OF  
THE VILLAGE WEAVER

## CHAPTER 2

### ASSOCIATIONS BETWEEN NESTING VILLAGE WEAVERS *PLOCEUS CUCULLATUS* AND OTHER ANIMAL SPECIES IN THE GAMBIA<sup>1</sup>

Moreau (1942) documents various associations that exist between African birds and other species at their nesting sites. He describes the colonial-nesting West African village weaver (*Ploceus cucullatus cucullatus*) as nesting in close proximity to raptors and humans in West Africa, and to wasps in the Caribbean, where this bird has been introduced. Moreau (1942) explained these associations in terms of predator avoidance.

In July and August 1999 we recorded observations of any animals discovered nesting or resting for over one hour within nesting aggregations of village weavers. We spent an estimated 500 person-hours observing 35 aggregations, which involved checking over 800 nests. Observations were conducted on and around Janjangbureh (Georgetown) Island in The Gambia. This island is approximately 18 km<sup>2</sup>, and is located on the Gambia River 300 km east of Banjul and the Atlantic coast. The island and the surrounding mainland are composed of Sahel scrub-savannah and gallery forest, interspersed with a small town, a few villages, and numerous plantations of rice, maize, bananas, and mangos.

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<sup>11</sup>This chapter is published as Lahti, D. C., Lahti, A. R. & Dampha, M. 2002. Nesting associations of the village weaver (*Ploceus cucullatus*) with other animal species in The Gambia. *Ostrich*, 73: 59-60.

*Wasps*

One old village weaver nest, 1 m high in a palm at the river's edge, was occupied by 15-20 wasps (cf. Moreau 1943). It was at least 2 m away from the nearest active nest, and in an area relatively sparse of nests. Other arthropods are also known to nest in association with weavers (Grimes 1973; Sharma 1991).

*Black cobra (Naja melanoleuca)*

Cobras were sometimes found in the center of winterthorn acacias where village weavers were nesting (cf. Maclean 1973). Two small overlapping acacias in the shallows of the river contained 30 village weaver nests near the periphery, and a 2 m-long cobra in the center (<2 m from most nests). A few nests contained eggs, and some others were in the process of being lined by the females, which they generally do 2-3 days before laying their first egg. Two days later a Gambian soldier ordered the cobra to be killed. Two days after that, no eggs were found in any of 8 nests that were checked, although all were lined. Whether this was a result of snake predation or human disturbance cannot be determined. Neighbouring acacias contained several weaver nests with undamaged eggs.

*Green mamba (Dendroaspis viridis)*

A thin, 0.7 m-long yellow-green to straw-coloured snake was found in a village weaver nest, 1.5 m above the ground at the edge of the river in a palm. Green snakes of the genus *Philothamnus* are very difficult to distinguish from a young mamba on sight (Villiers 1963: 113), but even young green snakes are generally darker dorsally than the snake we saw. The green mamba has been known to eat weaverbirds (Cansdale 1961:

34). There were no active weaver nests within 2.5 m, but two abandoned unlined nests were within 0.2 m of it. The nest with the snake was at one end of a 20 m stretch of about 80 nests loosely aggregated in three palms and an acacia.

*Boomslang* (*Dispholidus typus*)

A small (0.6-0.7 m) snake was discovered coiled in a weaver nest, and two local guides identified it as this notoriously poisonous but common species. The alternative would be an unusually slender egg-eating snake *Dasypeltis fasciata*. The boomslang is known to prey on weaver colonies (Collias and Collias 1971), as is the egg-eating snake (Cansdale 1961: 33).

*Green-backed heron* (*Butorides striatus*)

One winterthorn acacia in the shallows of the river housed 25-30 new village weaver nests, including some in construction. These were built around the perimeter of the tree, as is usual. In the center of the tree (0.5-1 m from the nearest nests) were four *Butorides striatus* nests, all with eggs. The adult herons were often in the tree among the village weaver nests. Four days later, three of the four heron clutches had hatched. A week after this, some of the neighboring village weavers had begun laying. *Butorides striatus* or their nests were found in several other trees containing village weaver nests, but none of these were observed breeding. Observations by Skead (1995: 898) in South Africa suggest that in these associations village weavers may follow and preferentially nest near breeding herons rather than vice versa.

*Yellow-backed Weaver (Ploceus melanocephalus)*

Yellow-backed weaver nests are smaller and of finer materials than those of the village weaver, as described in Barlow and Wacher (1997). In our study area they were always found within 5 m of the river and less than 1.5 m high, and were usually in the same low palms and acacias on the river's edge that the village weavers occupied. They were not found in dense village weaver colonies, nor in aggregations of more than 50 village weaver nests.

1. Three yellow-backed weaver nests were established along a 10 m stretch of broadleafed woody vegetation unoccupied by village weavers, but bordered at each end by a palm, one with a dense colony of >100 village weaver nests, and the other with 12 village weaver nests.

2. One yellow-backed weaver nest was found in a palm containing 20 village weaver nests. The yellow-backed weaver nest was surrounded on all sides but below by village weaver nests, the closest being 1m away.

3. Ten yellow-backed weaver nests were scattered over a 100 m stretch of riverbank in acacias, along with 12-15 village weaver nests. Over such a broad area, this grouping cannot even be called an aggregation. No single acacia held more than 3 nests, but at times both species were in one tree (1-2 m apart).

*Black-necked Weaver (Ploceus nigricollis)*

One palm on the river contained a pair of black-necked weavers, among 10 old village weaver nests, some new constructions, and two yellow-backed weaver nests. All nests were within an 8 m<sup>2</sup> area. This and the yellow-backed weaver were the only two weaver species seen to nest with the village weaver in our study site. Elsewhere several

other weavers have been observed in such an association with village weavers (Chapin 1954; Din 1992).

#### *Other birds*

Only once was a bird other than a village weaver observed coming out of a village weaver nest. Unfortunately the small drab bird (possibly an estrildid finch or sparrow) was not identified and did not return to the nest. Village weavers and other African weavers are known to nest in association with raptors (Moreau 1942; Maclean 1973; Walsh and Walsh 1976), but we did not observe this association.

#### *Mice*

Occasionally an old village weaver nest was found stuffed with finer nesting materials which protruded in various places. One such nest was found 2 m high over the ground 2.5 m inland from the river, and another 1m above that. The only nests within 2m were four old abandoned nests, one new nest and one in construction. A brown mouse (probably *Mus* sp.) leaped from the lower nest to the ground. No animal was in the higher nest. In a riverside aggregation in a palm of 9 village weaver nests and 3 constructions in progress, another mouse was found in an old nest. Like the previous mouse, it had filled the nest cavity with soft, fine materials, and left the nest when disturbed. The nest was 2.5 m high and 2 m from shore.

#### *Bats*

In one 50 m stretch of riverside thinly scattered with village weaver nests (many of them old and abandoned) and yellow-backed weaver nests, small (80-100 mm long)

brown bats were found in two adjacent newer nests hanging from vines, three in one nest and one in the other. Another nest contained 6 bats, apparently of the same species. The nest was 2 m high and 1.5 m from shore over the river, and was old and brown.

### *Humans (Homo sapiens)*

The village weaver's well-known propensity to nest in large colonies (100-300 nests) in the center of African towns and villages, despite man's predatory influence (Collias and Collias 1959), has given this bird its common name. In our study area, village weavers forage on rice and other grains in flocks of hundreds. Accordingly, large numbers of nests are built in the trees which border grain fields, along adjacent stretches of river, and along the irrigation ditches between the river and the fields.

Our observations suggest that village weaver aggressive displays and alarm calls are not likely to be reliable indicators of a negative (parasitic or predatory) relationship. No village weaver aggression was observed towards any species within their colonies, even known nest predators of village weavers. This indifference was particularly remarkable when weavers would incubate their eggs and engage in mating displays with a 2m-long cobra in their midst. Maclean (1973) suggested that sociable weavers *Philetairus socius* become quickly habituated to snakes in their nest mass, probably because the occurrence is so common. This habituation may be the case with village weavers as well. However, aggression was commonly observed among village weaver males towards each other, and to dummy models of village weavers and other birds placed so as to appear to be coming out of their nests (Lahti and Lahti, unpublished data). Moreover, the use of a village weaver nest by another species does not necessarily

indicate an eviction or predation of the village weavers by that species. Village weaver aggregations almost always contain nests, especially on their periphery, which are never accepted by females (see also Collias and Collias 1964). Often entire aggregations are abandoned with no further construction or destruction of nests.

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## CHAPTER 3

### **CACTUS FRUITS MAY FACILITATE VILLAGE WEAVER (*PLOCEUS CUCULLATUS*) BREEDING IN ATYPICAL HABITAT ON HISPANIOLA<sup>1</sup>**

#### *Abstract*

The village weaver (*Ploceus cucullatus*) is a bird usually found in moist areas, nesting near water and breeding during the rains. On Hispaniola I observed the village weaver breeding in the desert despite a lack of rainfall, and consuming the fruits of a columnar cactus *Stenocereus hystrix*. I propose that the carbohydrate and especially water content of these fruits may act as a "rainfall substitute", facilitating village weaver breeding in an arid environment. The village weaver may also affect plant community structure through seed dispersal.

The village weaver (*Ploceus cucullatus*: Ploceidae) is native to Africa but has been naturalized on several islands including Hispaniola (Lever 1987, Lahti in press). It nests in often dense colonies in a variety of habitats, most abundantly near agricultural fields and water sources (Bannerman 1949, Cyrus and Robson 1980, Maclean 1985, Raffaele et al. 1998, Lahti et al. 2002). Rice is the most significant element in the bird's

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<sup>1</sup>A shorter version of this chapter is in press in the *Wilson Bulletin*.

diet when it is available, and consistent availability of suitable grains, especially in the breeding season, is suggested to be an important factor limiting the size of village weaver populations (Da Camara-Smeets and Manikowski 1981, Adegoke 1983). The bird is absent from arid habitats; in fact, its native range in subsaharan Africa coincides with that portion of the continent which receives at least 1 mm of rain per day on average (Lahti in press). Rain has been found to be important in initiating colony formation and establishing subsequent breeding synchrony within the colony (Hall 1970). The length of the rainy season determines the length of the village weaver's breeding season (Da Camara-Smeets 1982).

During May-June 2001, I observed village weavers breeding in desert habitat in central Monte Cristi province of the Dominican Republic, where no rain fell for at least one month (pers. obs.). Local watercourses were dry and populated with cacti, and no standing water or agricultural fields existed in the vicinity of the breeding weavers. I located three large, dense aggregations (colonies: approximately 70, 70, and 150 nests respectively), one small aggregation (eight nests) and one large diffuse aggregation (approximately 100 nests) in trees of various species among stands of columnar pitayo cactus (*Stenocereus hystrix*). Cacti were generally found near or beneath trees. All weaver aggregations contained birds building, displaying, incubating eggs, and feeding nestlings. During May-June 2001 an estimated 70% of nests in all aggregations combined were active.

Village weavers were consistently observed feeding on the numerous ripe ovoid fruits of the cacti. They consumed pulp and juice along with the embedded seeds. Droppings from the weavers were frequent and distributed liberally over the ground and

foliage, especially from birds perched or flying within nesting trees. Droppings were watery, were colored red like the fruit, and contained small, black, intact seeds that were similar in appearance to those in the fruits. Ripe cactus fruits were splayed wide open by the feeding of the weavers (Fig. 3.1). No other birds were seen in the vicinity of the weaver nesting trees and cacti.

No previous reports exist of weavers feeding on cacti, but the fruits of *Stenocereus* and other columnar cacti (*Pilosocereus*, *Cephalocereus*, *Carnegeia*, *Neobuxbaumia*) are known to be food for wild birds (Raffaele and Roby 1977, Wendelken and Martin 1988, Silvius 1995, Godínez-Alvarez et al. 2002, Wolf et al. 2002). The fruits of *Stenocereus* spp. (called "pitayas" (Pimienta-Barrios and Nobel 1994)) are similar to prickly or cactus pears (*Opuntia*), which are also eaten by birds (Everitt and Alaniz 1981, Grant and Grant 1981, Le Houérou 1996). Although known frugivores like parrots (Psittacidae) and doves (Columbidae) dominate the records of cactus fruit consumption, birds of various families and diet types are also represented. Among these are a few finches which, like the village weaver, have bills adapted for granivory: Lesser Antillean bullfinch (*Loxigilla noctis*) (Raffaele and Roby 1977); varied bunting (*Passerina versicolor*), stripe-headed sparrow (*Aimophila ruficauda*) (Wendelken and Martin 1988); black-faced grassquit (*Tiaris bicolor*), vermilion cardinal (*Cardinalis phoenicius*) (Silvius 1995); *Geospiza* finches (Grant and Grant 1981); and house finch (*Carpodacus mexicanus*) (Godínez-Alvarez et al. 2002).

Weavers might compensate for the low availability of grains in the desert by exploiting the carbohydrate-rich *Stenocereus* fruit. In two dove species in the Sonoran Desert, more than half of incorporated carbon was found to come from saguaro

(*Carnegeia gigantea*) fruit (Wolf et al. 2002). Fruit of *Opuntia* has been found to be good in calcium, magnesium, and potassium relative to several noncactus subtropical fruits, but poor in other minerals and in protein (Everitt and Alaniz 1981). If the nutritional value of *Stenocereus* resembles that of other cacti, weavers would need to supplement this diet with protein sources such as arthropods, which they are known to eat in their native range (Adegoke 1983).

Perhaps more important to the weavers is the water source this fruit provides. *Opuntia* fruits are widely used as "drought insurance" fodder for cattle, as fruits even when aged one to three years retain 80% water content by mass (Le Houérou 1996). The water content of *Carnegeia* fruits has been suggested to be the reason why white-winged doves (*Zenaida asiatica*) can persist in the Sonoran Desert (Wolf et al. 2002). Given the strong dependence of the range and breeding season of the village weaver on rainfall and the usual proximity of their breeding sites to water sources, I hypothesize that the existence and breeding of this species in such an arid environment is facilitated by the water content of *Stenocereus*. If this is true, the breeding of weavers in this and perhaps other arid areas of Hispaniola should coincide with the periods when *Stenocereus* fruit is ripe. Moreover, at other periods in the phenology of these cacti, weavers should either cease breeding and range further afield to forage, or else abandon the deserts altogether and construct colonies elsewhere, such as around the ricefields common in central Dominican Republic. Succulent fruits may thus be a "rainfall substitute" for stimulating bird breeding and facilitating population persistence in an otherwise unsuitable habitat. This function is regularly performed by human provision in captive populations. Village

weavers, for instance, can be kept breeding all summer with a consistent food and water supply (Collias and Collias 1970).

Weaver foraging on cactus fruits could affect local plant community structure. The facts that the seeds appear to leave the weavers' digestive system intact, and that cacti were apparently clumped near large trees, suggest that the village weaver may accomplish seed dispersal for *Stenocereus*. Although these cactus fruits are unusual among tropical bird-dispersed fruits because they are too large to be swallowed whole, several features suggest adaptation for bird dispersal, including watery pulp, red color, and tiny seeds (Snow 1971, Wendelken and Martin 1988). Grant and Grant (1981) conclude that *Opuntia* dispersal is dependent on birds on Galapagos islands that are devoid of tortoises or iguanas. Silvius (1995) points out, however, that the sweet odor of ripe *Stenocereus* fruits suggests adaptation for mammal dispersal as well. The clustering of *Stenocereus* cacti beneath and around trees suggests dispersal by birds, since most weaver droppings fall from perch sites on trees. If *Stenocereus*, like some other columnar cacti, benefit from germinating in the relatively fertile and shaded microhabitat beneath a tree, this situation may represent an example of "directed dispersal" (Howe 1986). This would depend on many factors, including the dispersal capacity of the weaver, the distance to which weavers or secondary dispersers move seeds, and the degree to which *Stenocereus* is subject to density dependent mortality under weaver nesting trees.

The possibility of plant and bird breeding systems being coadapted is a common feature of evolutionary analyses of fruiting (Snow 1971, Rathcke and Lacey 1985). The village weaver has only been in Hispaniola for a couple of centuries. *Stenocereus* is not hypothesized to be adapted to weavers per se, however, but to generalized, even

opportunistic birds, of which the village weaver is probably the most relevant example on Hispaniola currently. The fact that the weaver is naturalized may in fact simplify tests of its relationship with *Stenocereus*. A significant challenge in this area of research is distinguishing direction of causation (Rathcke and Lacey 1985): correlation of fruit ripening with bird breeding may mean that either has influenced the other, or that both are influenced by a third factor such as rainfall or insect abundance. Initial observations suggest that pitayas facilitate weaver breeding, and that weavers disperse *Stenocereus* seeds near their nesting trees.



**Fig. 3.1. Ripe Fruit of *Stenocereus hystrix* in the Dominican Republic, Having Been Fed Upon by Village Weavers**

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## CHAPTER 4

### A CASE STUDY OF SPECIES ASSESSMENT IN INVASION BIOLOGY: THE VILLAGE WEAVERBIRD *PLOCEUS CUCULLATUS*<sup>1</sup>

#### *Abstract*

Application of recent insights gained in invasion biology to particular species may aid in addressing a central problem of the field, that of prediction of the dynamics of future introduction and invasion. The village weaverbird (*Ploceus cucullatus*) is concluded to be a potential invader of concern in several regions, especially the Mediterranean, Caribbean, and southeastern United States. This conclusion is supported by the introduction and invasion history of the species, factors concluded in recent reviews and quantitative studies to correlate with introduction success or invasiveness in birds, the species' agricultural pest status in its current range, and a published rating system. A proactive stance is recommended since control efforts have met with little success, but certain characteristics of the village weaver may provide opportunities for management.

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For decades ecologists have recognized the importance of invasive species, organisms that expand into a new geographical areas and subsequently spread from their points of entry (Elton, 1958; Williamson, 1996). A central theme in the political and scientific response to the invasive species problem has been a call for focused research on prediction of the likelihood of an invasion's occurrence and impact: the "Holy Grail of invasion biology" (Enserink, 1999). One way in which research may proceed in this area is to apply knowledge about particular candidate species and sites of potential introduction or spread, to our understanding of typical characteristics of invaders and invasion sites. This paper provides such a case study. The village weaver (*Ploceus cucullatus*) is a common passerine bird native to sub-Saharan Africa (Bannerman, 1949; Maclean, 1993; Barlow et al., 1997). The village weaver builds elaborate, enclosed nests in often dense colonies, and prefers the proximity of human habitation and agriculture (Collias & Collias, 1971; Lahti et al., 2002). Its ecological generalism and its successful establishment on islands to which it has been introduced, along with the agricultural damage it causes (e.g., Adegoke, 1983a; Manikowski, 1984), indicate it as an important candidate for applying recent work in invasion biology. Moreover, in the last two decades this species has been sighted with increasing frequency in the southern United States and Europe, which are outside of its current breeding range (e.g., Hipp, 1988; Pezzo & Morellini, 1999). This case study aims to (1) assemble what is known about the village weaver relevant to invasion biology, (2) assess the likelihood that this species will be an invader of concern in the future, and (3) determine whether its biology warrants actions to deal with ecological or agricultural problems.

## Regions of Past and Possible Future Naturalization

### *History of introductions and sightings*

The West African form of the village weaver (*P. c. cucullatus*) was introduced to the island of Hispaniola long before 1920, when the first specimens were collected (Wetmore & Swales, 1931). Most researchers believe that the village weaver is among those birds described by the eighteenth century historian Moreau de Saint-Méry as having been imported to Haiti from Senegal as cage birds (Wetmore & Swales, 1931). One source claims a colony to have been established in that country in 1783 (Long, 1981), and the species could have existed there before that time. By the 1930's the weaverbird was still mainly known from Haiti, and had only been found in two locations in western Dominican Republic (Wetmore & Swales, 1931; Bond, 1936). It remained at low densities on the island, and maintained its restricted distribution, through the middle of the twentieth century. As late as 1962 the Dominican Republic was not considered part of its range by Mayr & Greenway (1962). In the early 1960's, however, "a population explosion caused it to become so abundant that it became a serious pest to rice crops" (Long, 1981). Recently the species has been described as widespread and common in both countries on the island (Lever, 1987; Raffaele et al., 1998), although on no other island in the Greater Antilles. Some indication exists that the Hispaniolan population may be currently undergoing a decline, and some areas that have been known to support large colonies no longer do so (personal observation, IV-VI 01; J.W. Wiley, personal communication, III 01).

In about 1880 the western South African form of the village weaver (called there the spotted-backed weaver, *P. c. spilonotus*) was introduced to the Mascarene Island of

Réunion. In 1886 it was introduced to nearby Mauritius (Cheke, 1987; Jones, 1996). These introductions were probably due to escapes from captivity (Barré & Barau, 1982), and researchers are confident that no reintroductions have followed those events (Berlioz, 1946; Simberloff, 1992). As of 1946 the Réunion population was still restricted to the cultivated plains near the coast, but already had a reputation as an agricultural pest (Berlioz, 1946). By 1982 it was considered with the house sparrow (*Passer domesticus*) to be the worst agricultural pest on the island, and was abundant throughout the island in low elevations. On Mauritius the species spread slowly from its point of initial introduction (Cheke, 1987) and steadily increased in population size through the 1950s when it began to be considered a pest there as well.

Village weaver specimens were collected from the Cape Verde Islands off of the west coast of Africa in 1924 and a breeding attempt was documented in 1993 (Hazevoet, 1995). Their origin, and whether their presence there has been continuous or intermittent, is unknown, though they are usually presumed to be introduced (Long, 1981; Lever, 1987; Cramp & Perrins, 1994). A bird established on São Tomé Island has been claimed to be an introduced village weaver (Mayr & Greenway, 1962). In fact its origin is unknown, and differences in plumage from the mainland village weaver have led many to view it as a distinct species (Hall & Moreau, 1970; Naurois, 1994).

The first record of the village weaver nesting on Martinique was in 1980 (Pinchon & Benito-Espinal, 1980). The species was described as well established a few years later (Barré & Benito-Espinal, 1985). Though common, it is still reported to be localized in the same area to which it was introduced, at the northern end of the island (Raffaele et al., 1998).

In the past two decades the village weaver has been found in the wild for the first time in North and South America, and Europe. A single male was seen and photographed in South Carolina in 1988, apparently the first record from the continental United States (Hipp, 1988). The nearest population is 1600 km away on Hispaniola, but the bird could also have been an escape from captivity. The distance from Hispaniola to Florida is 750 km, although no records exist from that state. Hispaniola is of course close to other Caribbean islands, although the weaver is at most a vagrant in Cuba, Jamaica and Puerto Rico. (Despite the claim in Long (1981) and Lever (1987) that it exists on Puerto Rico, there is no support for this in the relevant regional works (e.g., Bond, 1936; Raffaele et al., 1998)). Recently the village weaver has been seen breeding in Venezuela (R. Restall, personal communication, VII 00). Specimens have been collected from the vicinity of Lake Maracaibo, which is 800km south of the Dominican Republic, or 1200km east-southeast of Martinique.

In Europe, the village weaver has been sighted at least six times in Italy, three of which involved breeding attempts (males building nests) (Pezzo & Morellini, 1999). Pezzo & Morellini (1999) suggest that the species may survive in the wild in Siena province, and could eventually become established in Central Italy. A breeding attempt has also been documented in the vicinity of Paris (Le Maréchal, 1985). These individuals survived the winter, which suggests that the species may be able to persist in that region. Other breeding attempts in the wild, some successful, are reported from France and Germany (Pezzo & Morellini, 1999). In Portugal breeding colonies have reportedly been established (Vowles & Vowles, 1994), although whether they persist is unknown. No sources are known for the birds in any of these localities, but they are often assumed to be

escapes. The distance from the northern African range limit to Portugal or Italy is approximately 2500 km.

In sum, three attempts at introduction are known in this species: Hispaniola, Réunion, and Mauritius. All of these were successful, although the Hispaniolan introduction is likely to have consisted of several events over a long period of time. One further naturalized population (Martinique) is of unknown origin. Establishment in Cape Verde, Venezuela, and Portugal is possible but not yet adequately documented. There are no known failed introductions of the village weaver, but escapes may have gone unnoticed, and village weavers have been sighted in many areas without becoming established. No single pattern of population growth characterizes the species in the several areas to which it has been introduced or spread. In the Mascarene Islands the populations have grown and spread steadily, whereas on Hispaniola the density remained low until a population boom and rapid spread occurred. On Martinique the population has grown but remained localized.

#### *Commercial bird trade*

The cage bird trade is probably responsible for much of the village weaver's existence outside of its native range; historical records indicate this method of introduction to the islands of Hispaniola, Mauritius, and Réunion over a century ago (Wetmore & Swales, 1931; Barré & Barau, 1982; Cheke, 1987). Data collected between 1974 and 1981 on annual exports of cage birds from Senegal, 13% of which were Ploceids, indicate France as the top importer. France, Spain, Belgium, Holland, Italy, and West Germany accounted for 75% of Senegal's bird trade during that period. The United States was a rising market, overtaking France in 1980 (Bruggers, 1983). However, in the

U. S. the village weaverbird in particular is said to be “seldom kept in captivity, mainly because of its aggressivity” (Hipp, 1988), and the captive populations that do exist are subject to legislated standards of confinement (Brosset, 1985). In France the species has been reported to be common merchandise and susceptible to escape due to lack of restrictions (Brosset, 1985). Some researchers believe that the village weaver’s recent establishment on the island of Martinique was due to recent bird trade (Barré & Benito-Espinal, 1985), whereas others see this species as one of several that may have been carried to the West Indies by storms from Africa (Norton, 1989; Wauer, 1996).

Given the nature of the Ploceid trade and the history of this species' introductions and sightings, the southern United States, the West Indies to northern South America, and southwestern Europe might be considered the regions of most probable introduction.

### **Factors Influencing Introduction and Invasion Success**

The ecology and behavior of the village weaver were determined from the literature and from observations of natural populations in its natural and introduced ranges during 1999-2001 (see, e.g., Lahti & Lahti, 2002; Lahti et al., 2002). These characteristics, along with habitat information from regions of most probable introduction, were compared with attributes of species and introduction sites that were found in recent reviews and quantitative studies to correlate with the likelihood of introduction success or invasiveness (Table 4.1). Here "introduction" refers to population establishment, whereas "invasion" refers to spread beyond the local area of introduction (Kolar & Lodge, 2001b). Both intrinsic and extrinsic factors were considered, in the sense of factors that respectively are or are not species-specific traits of the village weaver.

In general the village weaver fits the characterization of a successfully introduced and invasive bird as described by recent studies (Table 4.1). Of 14 factors found to correlate with introduction success in birds, 11 are consistent with success of the village weaver, at least in some regions of probable introduction. Of eight factors correlated with invasiveness for which relevant information about the village weaver exists, six are consistent with the village weaver. Intrinsic factors strongly favor both introduction success and invasiveness. The only thorough exception to this is plumage dimorphism, although migratory behavior and body mass appear to have opposite effects on introduction success versus invasiveness. The contribution of extrinsic factors is more ambivalent. The pattern of introduction is likely to consist of common releases of a very small number of individuals, and the likelihood of success also varies with the region of introduction. Two factors whose contribution is complex will be described in more detail: habitat and climate match, and competition.

#### *Habitat and climate requirements*

Successful introductions are associated with similarity of habitat and climate between the area of introduction and that to which the bird species is adapted (Kolar & Lodge, 2001b; Blackburn & Duncan, 2001). Although general indicators are quantitative and convenient, such as latitudinal differences and proportion of introductions in the same biogeographic region (Blackburn & Duncan, 2001), each bird species is likely to have particular habitat or climatic limitations. Among these can be elevation, ecosystem type, temperature, and precipitation.

The village weaverbird is not usually found above 300 m in elevation (Cheke, 1987; personal observation), although Clancey (1964) reports it to exist up to 1500 m in

KwaZulu-Natal, South Africa. Its tendency to be a lowland bird is especially evident on volcanic islands to which it has been introduced, such as Mauritius where even irrigated agricultural fields on the central plateau were devoid of colonies in early 2001. Elevation records are below 300 m in nearly all of the American southeast up to the Appalachians, and on several islands near Hispaniola, particularly Cuba. Large tracts of land exist within the village weaver's accustomed elevation range in the western and southern portions of the Iberian peninsula. Italy, which tends to be more mountainous, suggests that a naturalized population of the village weaver there might be more localized.

Landscapes converted from natural ecosystems to either development or agriculture are more likely to contain introduced birds (Case, 1996). Village weavers in particular exhibit diversity in their preference of ecosystem type. Their broad distribution in subsaharan Africa indicates the habitat generalism of this species (Bates, 1930). However, several generalizations hold throughout their range. On a local scale, they are most abundant near agricultural fields and water sources (Bannerman, 1949; Cyrus & Robson, 1980; Maclean, 1985; Raffaele et al., 1998; Lahti & Lahti, 2002). The village weaver is particularly noted for its tendency to dwell among human habitations, from which it may gain some protection from predators (Bates, 1930; Moreau, 1942; Da Camara-Smeets, 1982; Barré & Barau, 1982; Lahti et al., 2002). For example, Bates (1909) writes, "No sooner is a clearing made and stakes set in the ground for a new village than 'Benga'a' begin to build in the nearest tree... The more populous the village and the greater the hubbub of village life, the better are the birds pleased." They avoid dense forests, although they can be found in small woodlots or forests open enough to permit grasses. Most colonies I have observed were in trees, although in areas of

abundant food (e.g. near ricefields) they occasionally nest in shrubs or even herbaceous vegetation. The village weaver's prevalence in disturbed or agricultural lands is reflected in its reported range expansion in Africa over the last century, "due to the opening up of forests through increasing desiccation, fire, the relentless spread of human cultivation and the concomitant encroachment of savannah into what was previously homogenous forest land" (Crook, 1963: 222). Based on the habitats in which it has been most commonly observed, the village weaver seems well suited to Cuba and much of the southeastern U.S. (especially Florida, whose land is almost completely converted to development or agriculture). By the same considerations the largely agricultural European countries of Spain and Portugal, as well as southern France and Italy, provide appropriate village weaver habitat (data obtained from USDA NRCS (Natural Resources Conservation Service), 1992; SEI (Stockholm Environment Institute), 1999).

The village weaver is a tropical to subtropical species, so temperature may be a factor governing its distribution. A comparison of the village weaver's current global distribution with average annual temperatures and minimum annual temperatures of 30 cities in and near the bird's range (NOAA (National Oceanic and Atmospheric Administration), 1991) reveals that the village weaver tends to exist only near cities where the average annual temperature exceeds 20° C, and only where the minimum annual temperature is above 0° C. However, the village weaver has recently expanded its range into the vicinity of Gaborone, Botswana (Petersen, 1991; Herremans et al., 1994), where the minimum annual temperature does dip below freezing (-2° C in 2001). If temperature is a range-limiting factor in this species, various areas in the southern U.S.A. (southern half of Florida, south Texas, southwestern Arizona, and the coast of

California), and the Caribbean Islands fit the weaver's accustomed average and minimum annual temperature regime (CPC (Climate Prediction Center), 2002). In general the coastal areas of Spain and Portugal, the southern coast of France, and portions of the Italian coast (particularly near the French border and in the south) are also warm enough. Much of the interior of these countries, however, including Spain, dip readily below freezing. Nevertheless, an attitude of caution is still warranted in colder areas. The average annual temperature in Los Angeles, CA, U.S.A. is below 20° C, yet village weavers have survived and bred for years in aviaries there with no climate control, exhibiting no apparent variation in behavior with temperature fluctuation, except for more resting at higher temperatures (Collias et al., 1971). Moreover, temperature does not explain the absence of the weaver from many areas near its range which do have appropriate temperatures, such as much of Somalia, South Africa, and the northern Sahel.

The length of the rainy season determines the length of the village weaver's breeding season (Da Camara-Smeets, 1982). In fact, in the moister areas of Africa they breed in every month of the year and the males might never molt into their nonbreeding plumage (Chapin, 1954). There is evidence that rain is important in initiating colonies, and partly also in establishing subsequent breeding synchrony within the colony (Hall, 1970). Not surprisingly, therefore, precipitation provides a more accurate indicator of the range of the village weaver than temperature. For instance, a map of the village weaver's range in Africa coincides at all borders with a map of the areas which receive at least a millimeter of rain per day on annual average (GPCP (Global Precipitation Climatology Project), 2000). The precipitation contour explains, for instance, the village weaver's range in Southern Africa, which skirts Namibia and most of Botswana and terminates in a

finger curving along the eastern coast of South Africa. It also explains the weaver's absence from the region of Somalia southeast of the Red Sea, as well as the drier latitudes of the continent north of about 15° N. Comparing this one mm/day rule with the regions of probable introduction, all of the areas fit this criterion except for the far west of Mexico and the United States. Captive village weavers, of course, may breed all summer regardless of rainfall if provided with food, water, and nesting materials by caretakers (Collias & Collias, 1970). Likewise, in the uncommon case in nature where a dependable food and water supply and drought-resistant vegetation persist despite a lack of rainfall, village weavers may breed where they would not otherwise be expected. For example, in the Dominican Republic in V-VI 2001, weavers were observed breeding in large colonies in the northwestern desert, where the watercourses were completely dry and where no rain fell for at least a month, but where juicy cactus fruits were available and regularly consumed (personal observation).

Several areas of Europe and North America, then, in addition to the Caribbean, apparently provide appropriate climate and habitat for the village weaver, according to comparisons of elevation, ecosystem type, temperature and precipitation. Specifically, Florida and the Gulf Coast, much of Portugal, lowlying areas of Spain, southern France, and the northwestern and southern coastal areas of Italy fit the village weaver's current range in all these respects. Moving inland or northward from these areas tends to compromise one or more of the factors..

### *Competition*

Evidence suggests that competition with other introduced species may affect introduction success (Lockwood et al., 1993). This is difficult to test adequately

(Simberloff & Boecklen, 1991), and is likewise difficult to assess for any given species or region of probable introduction. With regard to the village weaver in particular, introduction success in the Mascarenes in the 1880's would have been considered unlikely according to the competition hypothesis, due to the high numbers of introduced species that already existed on those islands (Moulton et al., 1996). Despite competition, and despite a small propagule size, both introductions succeeded. Nevertheless, village weavers may yet encounter and be affected by competitors whose effects on their population size and invasiveness are difficult to predict.

The village weaver forms large foraging flocks and nesting colonies, and is often involved in synchronized competitive actions such as displacing other bird species in foraging areas and mobbing intruders near and within colonies (personal observation). Individually also they are aggressive, appropriately called “chasers and fighters” in one study (Din, 1992). The individual sighted in North Carolina was observed supplanting a boat-tailed grackle (*Quiscalus major*), a species over twice as long, at a feeder (Hipp, 1988). Together with its compact and enclosed nest structure, aggression in this species aids in defense against enemies such as brood parasites or predators (Collias & Collias, 1964; MacDonald, 1980; Din, 1992). These aggressive or competitive characteristics of the village weaver may enhance its establishment and population growth in new areas.

### **Agricultural Pest Status**

The extent of concern due to a potential invasive species and the necessity for proactivity depend not only on the species' likelihood of establishment and spread, but also on its probable ecological or environmental impact. The village weaver's habits of nesting in raucous colonies and denuding the vegetation have been troublesome in Africa

(Bates, 1930; Chapin, 1954; personal observation). There are also likely to be ecological effects of invasion that do not directly affect human economies. However, by far the most important and immediate concern in areas with village weaver populations is the effect of the bird's foraging in agricultural areas. From the earliest accounts of its behavior the species has been known as a destroyer of cereal crops in Africa (Bates, 1909; 1930) and Réunion (Berlioz, 1946). Recent accounts of the species in both its native and introduced ranges nearly always mention the damage it causes to local agriculture (e.g., Jensen & Kirkeby, 1980; Michel, 1992; Raffaele et al., 1998). This dietary preference has been supported by analysis of stomach contents, mainly in West Africa (Chapin, 1954; Adegoke, 1983a; Manikowski, 1984; personal observation). A recent survey of more than sixty evaluations of crop damage due to birds in West Africa has concluded that the village weaver is in some areas the single worst avian pest, and takes second place in the region as a whole, after the Red-billed Quelea (Manikowski, 1984). It is the biggest threat to agriculture in The Gambia, where a third of some farmers' rice crops have been destroyed (Lahti & Lahti, 2000). It has also been called the worst avian pest in Mauritius (Barré & Barau, 1982), and in Haiti, where losses of 20-35% to rice are sustained because of this species (Bruggers, 1983). An adult consumes on average 250 g of cultivated seeds in 30 days; one thousand birds therefore consume a third of the production of a typical Chadian field of sorghum in one month (Da Camara-Smeets, 1981).

An exception is South Africa, where the species is not considered a major pest (Craig, 1997). There are also regions such as central Uganda where weaver damage to crops has been relatively light (Kasoma, 1987). Determining the correlates of such

variation in crop damage could provide a basis on which to predict its probable impact in new areas. For instance, neither central Uganda nor eastern South Africa raise rice or similarly sized grains as a major crop, whereas a study in Nigeria found that rice was the most significant element in the bird's diet when available (Adegoke, 1983a). In fact, consistent availability of suitable grains, especially in the breeding season, is suggested to be the factor limiting the size of village weaver populations, and in turn, agricultural damage (Da Camara-Smeets & Manikowski, 1981; Adegoke, 1983a).

### **Smallwood-Salmon Rating System**

Smallwood & Salmon (1992) developed a rating system for invasive species which has been used to corroborate California's "most unwanted exotic species" list. The system utilizes questions about a species' invasive history and environmental impact to derive a series of values between 0 and 1 which estimate the relative probability of introduction, establishment, damage, and resistance to control methods. The village weaver's scores place it among the most dangerous invasive species, having the maximum total score of 27 (Table 4.2). These values, bolstered with the results of the application of recent studies, permit some bold suggestions. The village weaver may be predicted to have the red-billed quelea's (*Quelea quelea*) resistance to control, yet nearer to the starling's (*Sturnus vulgaris*) ease of introduction and establishment. No other exotic bird or mammal species in or near North America has this combination of strengths according to this rating system (Smallwood & Salmon, 1992). The rating system has not yet been applied in the literature to many species in or near other regions.

The rating system's final score results from a double weighting of establishment, and a triple weighting of damage and uncontrollability. Therefore, the post-invasion

impact of the species, regardless of its likelihood of introduction or invasion, is responsible for two thirds of the final score. Since the weaverbird is such a pest in its native range, the system may have inflated the invasiveness potential of this species on that basis. If an effective method were developed for control of the species, the adjustment to the final score would decrease it to 24. Nevertheless, the system is robust to changes in certain parameters: if the questions were answered such that the weaverbird was estimated to be two-thirds as damaging, or half as uncontrollable, the final score would not change.

### **Suggestions for Prevention and Control**

In light of the agricultural impact of the village weaver and its likelihood of invasion, proactive measures seem in order. Regulating the international trade of these birds is probably the best strategy (Brosset, 1985). Control methods such as fire, scarecrows, rattles, shooting, nest-robbing, and the felling of trees have not met with much success in Africa, the Mascarenes, or Hispaniola. Poison has been too expensive for most areas and is at best temporary anyway since local birds are responsible for most agricultural damage, and roaming populations can quickly fill in the gaps created by culls (Long, 1981; Adegoke, 1983b). Matters do not seem to have improved in this respect since Bates (1909: 44) noted that “the number killed by man does not seem to affect the population of the colonies. Killing numbers of them will not frighten them away, and tearing down their nests only makes them build the more furiously.”

The introduction history of this species suggests that, even where there is a population boom, there is a preceding period of lag (Sakai et al., 2001) where population sizes are low and probably more manageable. Therefore, in areas where new breeding

colonies are reported, proactive control methods, perhaps including removal of the population, may be advisable.

Given the village weaver's reliance on rain, those concerned with invasion might use rainfall and breeding season data from the species' current range to predict breeding seasons in new areas. For instance, Portugal receives very little rain between June and September, so village weavers introduced to that country will not be likely to breed during that time period. In general the one mm/day rule that on an average annual basis accords well with the species' range, also broadly matches the bird's breeding season when calculated on an average monthly basis (GPCP (Global Precipitation Climatology Project), 2000). This information can be useful in predicting what areas are likely to have longer breeding seasons, and therefore perhaps higher population growth, than others; it can also aid in maximizing efficiency of control methods in the event that they are required. Recall, however, that the provision of water and other resources to the weavers (e.g., by humans) can lead to an extension of their breeding season despite a lack of rain (Collias & Collias, 1970).

Much has been written on the pest status and control prospects of the top African bird pest, the red-billed quelea (e.g. Manyanza, 1983; Allan, 1983; Bruggers & Elliott, 1989; Mundy & Jarvis, 1989). Since this species has behaviors and agricultural impacts similar to those of the village weaver, building upon this research base and appropriating its results may aid in preparedness and control efforts for the more invasive village weaver.

<b>Extrinsic Factors</b>	<b>Studies</b>	<b>Consistent with VW?</b>	<b>Comments regarding probable influence on VW introduction and invasion success</b>
<i>Introduction success</i>			
More individuals released	KL 8/8	no	Introductions most likely from escapes, propagule size small
More introduction events	C, KL 5/7	yes	Several recent sightings in Europe and New World; active trade
Biogeographic region	BD	yes / no	Palaearctic high success / Nearctic low (Caribbean intermediate)
More human activity <sup>1</sup>	C	yes	VW associates with human settlement and agriculture (see text)
Less intersp. competition <sup>2</sup>	LMA	?	Competitors widespread; but VW a fierce competitor (see text)
<i>Invasiveness</i>			
More individuals released	KL 1/1	no	Introductions most likely from escapes, propagule size small
More introduction events	KL 1/1	yes	Several recent sightings in Europe and New World; active trade

<sup>1</sup>Case (1996) actually measured number of native extinctions, but considered this a proxy for “degree of human activity and habitat destruction and deterioration...”.

<sup>2</sup>Lockwood et al. (1993) actually measured morphological overdispersion of introduced relative to native species, which they consider to be an indicator of competition.

Factors in the first column exhibit a correlation with introduction or invasion success. In the second column, numbers following KL are the numbers of quantitative studies testing each factor (number of studies with a significant result / total number of studies), adapted from Kolar & Lodge (2001b) and subsequent adjustments (based on Sol, 2001; Kolar & Lodge, 2001a). These studies may not be independent tests of the hypotheses because four of the eight were of New Zealand birds. Other initials in the second column refer to the following studies: LMA = Lockwood et al. (1993), C = Case (1996), BD = Blackburn & Duncan (2001). No two studies had significant results opposed to each other.

**Table 4.1. Factors Correlated with Introduction Success and Invasiveness in Birds, and Relation to the Village Weaver *Ploceus cucullatus* (VW): (A) Extrinsic Factors.**

Intrinsic Factors on Introduction Success	Studies	Consistent with VW?	Comments regarding probable influence on VW introduction and invasion success
Higher body mass	KL 2/5 <sup>3</sup>	no	VW small (mass 31-45 g) (Maclean, 1985)
Plumage monomorphism	MMS, SMC, STL	no	VW conspicuously dimorphic
Lack of migration	KL 1/4	yes	VW not known to migrate (Crook, 1963; Adegoke, 1983a; Parker, 1999)
More broods per season	KL 1/2	yes	VW breeding season 3-12 months (Cyrus & Robson, 1980; Barré & Barau, 1982; Craig, 1997). Mean four breeding attempts in a 75-day period (Da Camara-Smeets, 1982).
Higher nest site	MMS	yes	VW usually nests 2-15m high throughout range (pers. obs.)
Broader diet	MMS	yes	VW eat seeds, insects (Adegoke, 1983a), and fruit (pers. obs.).
Commensalism with humans	STL	yes	VW associates with human settlement and agriculture (see text)
Larger geographic range size	BD	yes?	Introduced birds range from 0.25 to 68625 degrees <sup>2</sup> , mean 1386 (T. M. Blackburn, pers. comm.). VW range ~3715 degrees <sup>2</sup> .
Better habitat/climate match	BD <sup>4</sup> , KL 1/1	yes	E.g., West Indies, southern U.S., and Mediterranean (see text)
Successful introduction history <sup>5</sup>		yes	Established in three of three known introductions; but failed introduction events (escapes) may go unnoticed.

<sup>3</sup>Both of the two significant studies had mixed results (Sol, 2001).

<sup>4</sup>Blackburn & Duncan (2001) actually measured latitudinal difference and proportion of introductions within the same biogeographic region as the source population, but considered these proxies for “climatic and habitat features”.

<sup>5</sup>No quantitative study has tested whether successfully established or invasive exotic birds tend to become established or invasive in subsequent introductions as well. The factor is included here because of its plausibility (Simberloff & Boecklen, 1991; Vermeij, 1996).

See caption on previous page. Other initials in the second column refer to the following studies: SMC = Sorci et al. (1998), MMS = McLain et al. (1999), STL = Sol et al. (2002). No two studies had significant results opposed to each other.

**Table 4.1. Factors Correlated with Introduction Success and Invasiveness in Birds, and Relation to the Village Weaver *Ploceus cucullatus* (VW), continued: (B) Intrinsic Factors on Introduction Success.**

<b>Intrinsic Factors on Invasiveness</b>	<b>Studies</b>	<b>Consistent with VW?</b>	<b>Comments regarding probable influence on VW introduction and invasion success</b>
Presence of migration	KL 1/1	no	VW not known to migrate (Crook, 1963; Adegoke, 1983a; Parker, 1999)
Smaller body mass	KL 1/1	yes	VW small (mass 31-45 g) (Maclean, 1985)
Smaller egg mass	KL 1/1	yes	VW small (initial mass 2.3-3.6 g: $N=94$ clutches)
Shorter juvenile period	KL 1/1	?	Juvenile period uncertain for VW
More broods per season	KL 1/1	yes	VW breeding season 3-12 months (Cyrus & Robson, 1980; Barré & Barau, 1982; Craig, 1997). Mean four breeding attempts in 75-day period (Da Camara-Smeets, 1982)
Greater longevity	KL 1/1	?	Longevity uncertain for VW
Better habitat/climate match	KL 1/1	yes	E.g., West Indies, southern U.S., and Mediterranean (see text)
Successful invasion history <sup>5</sup>		yes	Invasive in three of three known introductions; but at least one noninvasive naturalized population exists.

<sup>5</sup>No quantitative study has tested whether successfully established or invasive exotic birds tend to become established or invasive in subsequent introductions as well. The factor is included here because of its plausibility (Simberloff & Boecklen, 1991; Vermeij, 1996).

See caption on page before last.

**Table 4.1. Factors Correlated with Introduction Success and Invasiveness in Birds, and Relation to the Village Weaver *Ploceus cucullatus* (VW), continued: (C) Intrinsic Factors on Invasiveness.**

	<b>Village Weaver</b>	Pig	House Mouse	Monk Parakeet	House Sparrow	Starling	Quelea
Introduction	<b>0.6</b>	0.82	0.93	0.89	0.64	0.57	0.37
Establishment	<b>0.75</b>	1	1	0.75	1	1	0.25
Damage	<b>0.75</b>	0.89	0.84	0.64	0.66	0.81	0.72
Uncontrollability	<b>0.84</b>	0.43	0.41	0.54	0.41	0.41	0.84
Total rating	<b>27</b>	27	27	27	27	26	21

Values in the interior of the table range from 0 to 1, with a high score representing a high rating of concern in the respective area. Total values (bottom row) range from 9 to 27, with high scores denoting species of generally high concern as invaders. Other known invasive species are provided for comparison with the village weaver.

**Table 4.2. Expected Ratings of Concern for Invasion, According to the Smallwood-Salmon Rating System (Smallwood & Salmon 1992)**

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PART II

THE EVOLUTION OF DEFENSES AGAINST BROOD PARASITISM IN THE  
VILLAGE WEAVER

## CHAPTER 5

### HOW PRECISE IS EGG DISCRIMINATION IN WEAVERBIRDS?<sup>1</sup>

#### *Abstract*

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 behavior according to egg appearance differences by logistic regression. Results supported all three hypotheses. We estimated

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<sup>1</sup>This chapter is published as Lahti, D. C. & Lahti, A. R. 2002. How precise is egg discrimination in weaverbirds? *Animal Behaviour*, 63: 1135-1142.

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.

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 extra-pair copulation and brood parasitism can decrease the reliability of such rules. For instance, in a species 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 defense against brood parasitism is provided by studies which 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 varying widely in appearance between individuals, such as the *Ploceus* weaverbirds (Moreau 1960). In these species a cuckoo 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 two to nine 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 and 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 and 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 and Wiley (1989) and Robert and 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 diederik 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 at the time of parasitism aids a village weaver in distinguishing a foreign egg as such, this suggests that the mechanism of *recognition by direct comparison* is being utilized to some extent.

Egg shape and mass vary more among an individual's eggs than do 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 between July-August 1999. This time period was during the breeding season of the village weaver and the diderik cuckoo. Wetmore and 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 centers of towns and villages. 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 0.6m to 10.7m in height, which was also the range of our study nests (mean=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 800 and 1200 h. Study nests were unmarked; a numbered tag was placed >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 24-28h 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.

Since 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 of females 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 d. Eggs with no or very small embryos were translucent. In cases where eggs were not translucent (older eggs, and some with dark colour and speckling), the egg to be replaced was broken open to estimate embryo age. 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. Each 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*

Egg colour was determined 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; Collias 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 (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.

Four variables relating to egg speckling were assessed: 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 5.1). 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

(ARL) performed all egg colour and speckling assessments before results were taken. Blind reassessments by ARL and independent assessments by DCL 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 (LR) (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 and 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 appearance between the foreign egg and the host's own egg (LR:  $N=71$ ,  $P<0.0001$ ,  $Sns=0.72$ ,  $Spc=0.79$ ,  $R=0.36$ ). (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 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 includes the degree of difference in egg colour and the interaction of spot density with spot aggregation at the egg cap (LR:  $N=71$ ,  $P<0.0001$ ,  $Sns=0.63$ ,  $Spc=0.73$ ,  $R=0.30$ ; Table 5.2). In this interaction a response to a difference in spot density is more pronounced when accompanied by a difference in cap aggregation, and vice versa.

The odds ratio is an easily interpretable measure of the parental response to differences in colour and speckling (Table 5.2). For instance, egg colour difference is 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 indicates that an experimental egg is on average twice as likely to be rejected when it differs from the host's egg in speckling than when it is similar. Speckling variables were continuous (Fig. 5.2), but are represented here as binary solely for convenient interpretation of the odds ratio.

A model including only egg colour differences predicts egg rejection well (LR:  $N=71$ ,  $P<0.0001$ ,  $Sns=0.60$ ,  $Spc=0.70$ ,  $R=0.21$ ; Fig. 5.1), as does the best model with only speckling variables (LR:  $N=71$ ,  $P<0.0001$ ,  $Sns=0.58$ ,  $Spc=0.69$ ,  $R=0.15$ ), although speckling differences explain 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 5.2). No significant interaction between colour and speckling variables exists in any model, indicating that the birds assess colour and speckling independently.

With regard to speckling, multivariate analysis does not suggest that any single variable, or any single interaction, is clearly most important. Rather, differences in spot colour, size, density, and cap aggregation are correlated with each other. Replacing spot density with spot size in the best model, for instance, yields a model with only a slightly worse fit. Among univariate tests of speckling variables, spot density best predicts egg rejection (LR:  $N=71$ ,  $P=0.019$ ,  $Sns=0.47$ ,  $Spc=0.61$ ,  $R=0.03$ ; Fig. 5.2), yet is far inferior to the multivariate speckling model. Therefore, although the birds are assessing differences in speckling, they may be 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 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 and Wiley (1989) and Robert and 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 is evident in our study population, over which eggs are rejected. Rather, the data is 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 are 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 (1972) with this species and Rothstein (1975) 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 utilized at all. This precise ability is adaptive in this species relative to the other two alternatives on account of the small clutch size. Rejection by discordancy is a futile strategy in 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 diederick cuckoo removes an egg when parasitizing (Friedmann 1968), some birds, especially young ones, do not have the opportunity for direct comparison when parasitized, since 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 exhibits a range of egg colour variation which approaches that of the population as a whole (Din 1992; Lahti and Lahti, unpublished data); this lack of geographical variation in egg color 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 nonselective processes have resulted in high variability in egg appearance (Moreau 1960). If this is the case, whether an individual 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 which can

mimic eggs (as the diederik cuckoo does (Payne 1967)) or conspecific brood parasitism (as occurs in a close relative (Jackson 1992)), or both.

<b>Variable</b>	<b>Measure</b>	<b>Field estimation</b>	<b>Quantitative (index) value</b>
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 # 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.

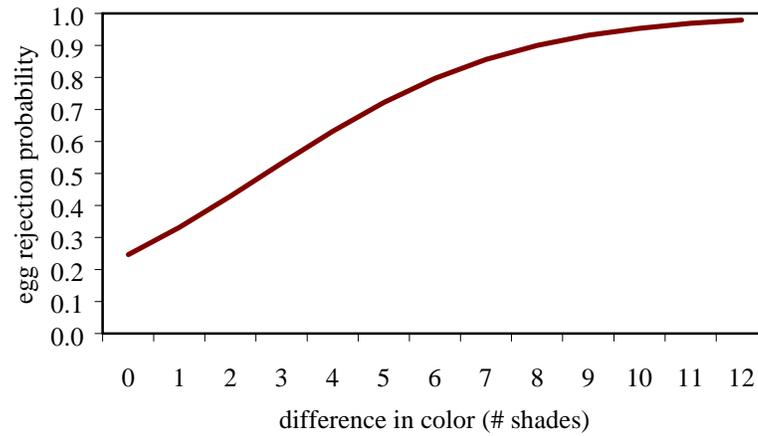
**Table 5.1. Quantification of Egg Speckling Variables by Indexing**

<b>Parameter</b>	<b>Estimate</b>	<b>S. E.</b>	<b>t-Ratio</b>	<b>Odds Ratio (95% C.I.)<sup>b</sup></b>	<b>P</b>	<b>R</b>
(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 <sup>a</sup>	-0.33	0.35	-0.93	0.72 (0.36, 1.44)	0.3	0.013
Cap aggregation <sup>a</sup>	-0.22	0.35	-0.63	0.80 (0.40, 1.60)	0.5	0.020
Spot density x Cap aggregation	0.79	0.36	2.19	2.20 (1.09, 4.47)	0.028	0.076

<sup>a</sup>Main effects are retained even when nonsignificant, when their interaction is significant.

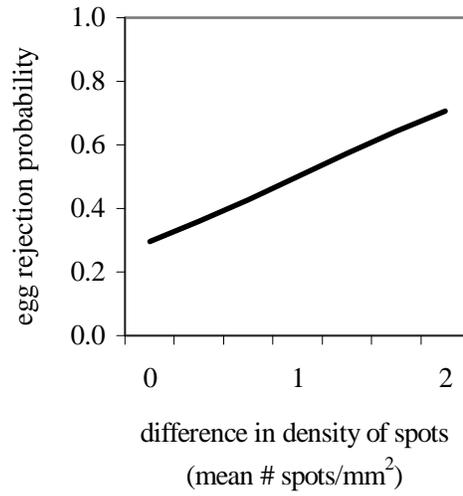
<sup>b</sup>The Odds Ratio estimates how much more likely egg rejection is with one unit increase in the parameter. For ease of interpretation, the odds ratios here for the speckling variables are based on a binary coding (difference = 0 / difference > 0).

**Table 5.2. Parameters of Multiple Logistic Regression Model, Predicting Egg Rejection on the Basis of Egg Colour and Speckling Differences Between Host and Foreign 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.

**Figure 5.1. 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.

**Figure 5.2. Weaverbird Rejection of Experimental Eggs by the Difference in Spot Density Between Host and Experimental Eggs**

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## CHAPTER 6

### EVOLUTION OF EGG APPEARANCE FOLLOWING A CHANGE IN SELECTIVE REGIME

One of the few rigorous ways to detect the action of natural selection in the wild is to perturb a population's environment and observe a predicted change in a trait (Endler 1986). A few researchers have observed trait evolution after a species was introduced into a new environment whose selective regime on the trait differed markedly from that of the source environment. Magurran et al (1992) and Reznick et al. (1997) demonstrated rapid evolution of antipredator behavior and life history traits respectively, following independent experimental introductions of guppies (*Poecilia reticulata*) into drainages that differ in predation risk from the source drainages. Losos et al. (1997) introduced the lizard *Anolis sagrei* into several small islands in the Bahamas that had not previously been populated with *Anolis*. Although the researchers intended to study patterns of extinction, they discovered clear morphological differentiation of the introduced forms after little more than a decade. Limb morphology was correlated with vegetational structure of the various islands as expected based on *Anolis* morphology throughout the Caribbean.

The results of Losos et al. (1997) highlight the fact that an introduction event need not be an intentional initiation of a test of an evolutionary hypothesis for it to function as

one. In fact, any historical introduction of a species can initiate such a test, as Grinnell (1919) noted when he called the introduction of the house sparrow (*Passer domesticus*) into the United States an "experiment in nature". In a well-known study, Johnston and Selander (1964; 1971) later found support for Allen's, Bergmann's, and Gloger's adaptive ecogeographic rules in the differentiation of North American house sparrows.

Evolutionary change has been documented in several other introduced species (Berry 1964; St. Louis & Barlow 1991; Baker 1992), but in most cases adaptive explanations are elusive or tend to be *ad hoc*, as pointed out by Berry (1996). Evidently, the introduction of a species rarely happens to facilitate a rigorous prediction of the action of natural selection on a trait, or else existing opportunities have gone unexamined.

The village weaverbird (*Ploceus cucullatus*), a common passerine of subsaharan Africa, was introduced from West Africa to the Caribbean island of Hispaniola during the colonial period, probably before the 1790s in a series of introductions over several decades. The same species was also introduced from Southern Africa to the island of Mauritius in a single event in 1886 (Lever 1987; see Chapter 4). No reports exist of later introductions into either population. On both islands the bird is presently abundant and experiences no known gene flow with other populations (Fig. 6.1).

In Africa the village weaver is a regular host of the brood parasitic diderik cuckoo (*Chrysococcyx caprius*) (Morel & Morel 1962; Payne in press), a species whose eggs mimic weaver eggs (Chapin 1954; Jensen & Vernon 1970; Payne in press), and whose chicks generally hatch early and remove any weaver eggs from the nest (Payne 1967; 1977).

Weavers of the genus *Ploceus* lay eggs whose variability in appearance between

females is among the highest among birds (Moreau 1960; Schönwetter 1983; Freeman 1988; see Fig.6.2). The color and spotting pattern of an individual female's eggs are consistent over her lifetime (Collias 1984). Bates (1911) first suggested that the high variability of egg appearance in the village weaver might function in discrimination against foreign eggs. Victoria (1972) showed that captive village weavers do eject foreign eggs from their nests. Recently, Lahti & Lahti (2002) experimentally tested egg discrimination of village weavers in West Africa. Village weavers reject foreign eggs from their nests in proportion to the difference in color and spotting pattern between the foreign eggs and their own. Females remember the appearance of their eggs during a nesting attempt, such that they do not need one of their eggs in the nest at the time of parasitism to discriminate effectively.

Egg discrimination and rejection allow a host to avoid much of the cost of cuckoo brood parasitism (Payne 1997). However, the closer a foreign egg is to an individual's own eggs in spotting pattern or color, the more likely she is to fail to distinguish it as foreign (Lahti & Lahti 2002). Given that successful cuckoo parasitism nullifies a weaver's reproductive attempt, and that a weaver is further manipulated into providing parental care for the cuckoo chick until it is independent, natural selection for egg discrimination is expected to be intense where cuckoo parasitism is a consistent threat (Davies & Brooke 1989a).

In order for egg discrimination to function in the context of parasite egg mimicry, host egg appearance must contain reliable signature information, as objects of recognition must in general (Beecher 1991). In particular, egg appearance must be consistent within a clutch, and distinctive within the population. Davies and Brooke (1989b) developed the

hypothesis that bird clutch uniformity might be maintained by natural selection for egg recognition, although the hypothesis was implied earlier by Bannerman (1949) and Collias (1984) in reference to village weavers. Precise consistency of egg appearance within a clutch ensures that only a narrow range of eggs will be acceptable as one's own, which minimizes the window of opportunity for a prospective parasite. Davies and Brooke (1989b) and Stokke (1999) tested human subjects' perceptions of clutch uniformity in hosts of the common cuckoo *Cuculus canorus*. Davies and Brooke (1989b) did not find an effect. Stokke et al. (1999) found that birds whose clutches were ranked as more uniform were more likely to peck at artificial blue eggs in their nests. Intraclutch variation in egg color and spotting has been assessed in several bird species, but all known studies of color and nearly all of spotting (exceptions: Baerends & Drent 1982; Brown & Sherman 1989) use subjective methods that do not allow comparison. Distinctiveness of egg appearance relative to the rest of the weaver population would also tend to undermine parasite egg mimicry, since cuckoos maximize their fitness by producing eggs that resemble common host egg morphs (Baker 1913; 1942). Polymorphism in egg appearance has been shown to aid egg recognition in a number of species (Tschanz 1959; Victoria 1972; Moksnes 1992), although none of these studies are quantitative. Features of egg appearance that hosts use in discriminating their own eggs from foreign ones are thus expected to exhibit low within-clutch variation, and high population-level or between-individual variation. These two factors determine reliability of signature information.

This study tests four predictions from the hypothesis that egg appearance in the village weaver is maintained by natural selection primarily as a counteradaptation to

interspecific brood parasitism. (P1) Since egg color and spotting are the features of egg appearance used in egg discrimination (Lahti & Lahti 2002), color and spotting should provide reliable signature information in African populations of the village weaver where egg-mimicking cuckoo parasitism occurs. Other egg appearance features not used in egg recognition in this species, such as egg shape and mass, should be less effective signatures. (P2) The reliability of egg appearance signature information should be lower on the island of Mauritius devoid of cuckoo parasitism, than in the South African population which was the source of the Mauritian population over a hundred years ago. (P3) The reliability of egg appearance signature information should be lower on the island of Hispaniola, on which there is also no egg-mimicking brood parasite, than in the West African population that was the source of the Hispaniolan population over 200 years ago. (P4) The differences in signature reliability should reflect time since divergence; specifically, the difference in signature reliability between the Mauritian and South African populations should be less than that between the Hispaniolan and West African populations because the Hispaniolan lineage has been evolving in the absence of cuckoo parasitism for at least twice as long as the Mauritian lineage.

Decay of nonfunctional traits is to be expected eventually by "disuse, aided sometimes by natural selection" (Darwin 1859: ch.15). Loss of a trait may or may not be hastened by direct selection (the vestigial feature hinders reproductive success, even if merely through poorer energy economy), or indirect selection (such as through antagonistic pleiotropy). Otherwise evolution may proceed in a different direction, or the genes underlying the trait might be subject to the accumulation of neutral mutations (Prout 1964; Fong et al. 1995).

No study has assessed costs of clutch distinctiveness or uniformity, which would help to determine whether loss of egg distinctiveness and clutch uniformity would be adaptive in the absence of cuckoo brood parasitism. For instance, the maintenance of similarity within a clutch could involve costly precision in the application of pigment from egg to egg. Distinctiveness of egg appearance within the population, likewise, might require the production of pigment concentrations or combinations that bear some physiological cost relative to pigment production in a historically unparasitized population.

Whether or not the mechanism is understood, evolution of a trait following a change in selective regime sometimes proceeds very rapidly. For instance, Heath et al. (2003) removed salmon from wild populations in which predation risk favored large egg size. After 13 years in captivity, egg size had decreased by 25% through evolution. Rapid evolutionary decay of traits following a reduction in selection for their functionality has also been found in *Spartina* cordgrass (~100 years: Daehler & Strong 1997) and *Poecilia* guppies (~32 years: Magurran et al. 1992). One lesson from theory and empirical research is that selection can act cryptically, such as through pleiotropy which is probably more widespread than is generally recognized (Wright 1964; Alexander 1990; Thaker & Kankel 1992). Also, the accumulation of neutral mutation by itself does not seem to be able to account for trait loss in many contexts, particularly in a short period of time (Wright 1964; Prout 1964; Fong et al. 1995).

Although observations of traits in source and introduced populations were synchronic in evolutionary time, no indication exists that the source populations in Africa have experienced changes in the selective regime imposed by the diederik cuckoo during

the period since divergence from the introduced populations. Therefore the present selective regime and trait values in the two African populations are interpreted here as an approximation of those of the ancestors of the Mauritian and Dominican populations. Results will be presented as though the trait values are allochronic rather than synchronic (Hendry & Kinnison 1999), and therefore represent anagenesis, an evolutionary pattern on which there are far fewer empirical data than cladogenesis.

## **METHODS**

### **Egg Collection**

I collected complete clutches of the village weaver within one to three days of clutch completion, from the following localities: Janjangbureh Island, The Gambia, West Africa (13°35'N, 14°40-50'W; VII-VIII 1999; N=107); Pietermaritzburg, KwaZulu-Natal, South Africa (29°25-45'S, 30°25-35'E; X-XII 2000; N=122); Black River and Rivière du Rempart Divisions, Mauritius (20°00-20'S, 57°20-40'E; XII 2000 - II 2001; N=52); and Monte Cristi and Valverde Provinces, Dominican Republic (19°35-45'N, 71°00-20'W; IV-VI 2001; N=154). Hereafter G<sub>s</sub>=The Gambia and SA<sub>s</sub>=South Africa (two source ranges); M<sub>i</sub>=Mauritius and DR<sub>i</sub>=Dominican Republic (two introduced ranges) (Fig.6.1).

Clutches varied between one and four eggs, and average clutch size varied across study sites. So as not to bias analyses of variability by site differences in average clutch size, analyses were based on two random eggs from clutches greater than two eggs, so all within-clutch analyses are based on 'effective clutches' of two eggs. One-egg clutches were excluded from within-clutch variability analyses.

Removal of eggs had a negligible impact on the seasonal reproduction of the

individuals involved and on the persistence and activity of their breeding colonies. Nest predation occurs at a high rate in village weavers (personal observation); accordingly, females renest rapidly after the loss of a clutch and raise several broods in a breeding season, which is often more than half a year in duration (see Chapters 3, 4). On average, fewer than 10% of nests were disturbed from each colony visited, and females from nearby nests generally returned to incubate their eggs within 5 min after researchers withdrew. In each study area village weavers are among the most abundant bird species in the region. The species is considered the worst avian agricultural pest in The Gambia, Mauritius, and the Dominican Republic due to its preference for cultivated grains (see Chapter 4).

### **Measurements**

For each of the following egg characteristics, all measurements across all study sites were performed by a single person (ARL or DCL).

#### *Egg shape and mass*

We measured length and breadth of each egg with digital calipers to the nearest 0.1 mm. Shape was considered to be the ratio of length to breadth. Mass was measured to the nearest 0.05 with a spring scale.

#### *Eggshell ground color*

We assessed eggshell color by direct comparison with the *Villalobos Color Atlas* (Villalobos-Dominguez & Villalobos 1947), which has been used to assess egg color variation and its inheritance in a captive population of village weavers (Collias 1984, 1993) and to assess egg color differences required for egg rejection in this species (Lahti

& Lahti 2002). 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 (Villalobos-Dominguez & Villalobos 1947), are hue (the color of the pigment), brightness or value (the position on a scale of light to dark), and chromaticity or degree (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 colored 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 two remaining variables, brightness and chromaticity.

Color charts assume that color differences perceived by humans are equivalent to differences perceived by birds. This assumption is questionable, especially since birds have more and different cone types than humans and can see light in near-UV wavelengths (300-400 nm) (Bennett et al. 1994; Cuthill et al. 1999). Therefore I also measured eggshell reflectance with an Ocean Optics USB2000 UV-VIS spectrophotometer and OOIBase32™ software (©1999 Ocean Optics, Inc., Dunedin, FL). 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 ms. I standardized measurements with a diffuse tile made of PTFE that reflects >98% of light over all sampled wavelengths (Ocean Optics WS-1). I performed all measurements under an opaque cloth because ambient light affected the readings otherwise. For examples of eggshell spectra see Figs.6.3, 6.4. A few eggs lacked

uniformity in color, in which cases I analyzed the spectra that characterized the largest proportion of the egg's surface area.

I reduced reflectance comparison data using principal components analysis (PCA) (Jolliffe 1986). Perhaps due in part to the curvature of eggs, reflectance measurement error was high enough (SD of ten measurements of the same egg=5.6%) to swamp typical within-clutch differences in egg color (e.g., avg. SD of a clutch in The Gambia=3.6%). Therefore, only color chart data were used for within-clutch analyses. For between-clutch analysis, PCA reduced the variation in the data into three orthogonal principal components. PC1 explained 70.4% of the variance in the sample. It loaded consistently across the entire (300-700 nm) range of wavelengths, and therefore corresponds closely to brightness, consistent with Endler (1990). PC2 explained 6.2% of the variance, and represents chroma and hue, mainly contrasting blue-green with other colors. PC3 explained 2.5% of the variance and is also representative of chroma and hue, contrasting reflectance in high (reddish) vs. low (bluish) wavelengths.

### *Eggshell spotting*

We measured eggshell spotting as four variables: size, density, color, and the degree of aggregation at the cap (broad) end of the egg. For each parameter we initially grouped all eggs that possessed spots subjectively into three categories in the field. I then obtained quantitative measurements of five representative eggs from each category. For these eggs, spots entered the analysis if they were visible at 10x power in a dissection microscope. The village weaver, like some other birds with spotted eggs, alternate deposition of spots and ground color, such that some (secondary) spots are pale because they are deposited before the final layer of ground color, whereas other (primary) spots

are brighter because they are deposited after the final ground cover deposition (Baerends & Drent 1982). Both primary and secondary spots were considered when they could be distinguished. For spot size, density, and cap aggregation measurements, a 35 mm<sup>2</sup> area in the longitudinal center of the egg was sampled for each representative egg. This area was trapezoidal in shape and positioned to avoid sampling bias along the longitudinal axis of the egg (Baerends & Drent 1982).

For spot size, I measured the area (length x width) of all spots in a 35 mm<sup>2</sup> area, and calculated the average spot area per egg (Fig.6.5). For spot density, I counted the spots in a 35 mm<sup>2</sup> area and calculated average number of spots/mm<sup>2</sup> (Fig.6.6). For spot color, I chose representative eggs with the largest spots, and assessed reflectance of a primary spot from each egg with the spectrophotometer (Fig.6.7). For spot cap aggregation, I counted the number of spots in a 35 mm<sup>2</sup> area on the cap of the egg, with the number in a 35 mm<sup>2</sup> in the longitudinal center of the egg. The degree of cap aggregation was described by the proportion  $1 - (D_{\text{center of egg}}/D_{\text{cap}})$ , where  $D$  is the average spot density in spots/mm<sup>2</sup>. This yields a range of 0 to 1, the two theoretical extremes being eggs whose spots are all on the cap (1), and eggs whose spots are distributed evenly over the egg (0) (Fig.6.8). For each spotting variable, I calculated the mean value among the five representative eggs for each of the three levels of the variable.

By using this indexing method of spot variable assessment, we avoided the prohibitive labor of taking spot measurements of every egg in our sample, while avoiding also the incommensurability of subjective ranking alone. The resulting variables from this method are properly coded as categorical in statistical analysis. Despite this, we can estimate an underlying continuous scale of measurement (Figs.6.5-6.8), which facilitates

interpretation and comparison among species and studies.

### **Statistical Analysis**

Data analysis was performed using SYSTAT<sup>®</sup>10.0. Within-clutch variance for a given variable was the disparity between the two eggs in each effective clutch. All eggs in each population sample were then paired at random using the random number generator in Microsoft Excel<sup>®</sup>. Mean between-individual variance was the mean disparity between the randomly paired eggs. Reliability of signature information was determined by comparing the within-clutch vs. between-individual disparity in a population, and by comparing the proportion of total variation in the population that was accounted for by within-clutch vs. between-individual variation.

Comparisons within and between populations were analyzed using ANOVA for continuous variables (e.g., egg color, size, shape), and interpopulation pairwise comparisons were Bonferroni adjusted. The Kruskal-Wallis/Mann-Whitney *U* test was used for categorical variables (e.g., egg spotting). Levels of significance in the M-W *U* test can be distorted when there are too many tied values, which are common in the spotting variables. Spotting disparity within clutches was therefore also recoded as binary (difference/no difference) and analyzed by Chi-squared ( $\chi^2$ ) test for independence. All statistical tests are considered significant at  $P < 0.05$ .

## **RESULTS**

### **Egg Shape and Mass**

For both source populations, egg shape and mass were significantly more variable between individuals than within clutches, as was the case for all other egg appearance

variables. This difference was greater for egg mass (ANOVA:  $F_{1,152}=50.7$ ,  $P<0.00001$ ,  $R^2=0.25$  ( $G_s$ );  $F_{1,190}=42.6$ ,  $P<0.00001$ ,  $R^2=0.18$  ( $SA_s$ )) than for egg shape (ANOVA:  $F_{1,153}=18.8$ ,  $P=0.00003$ ,  $R^2=0.11$  ( $G_s$ );  $F_{1,177}=12.0$ ,  $P=0.0007$ ,  $R^2=0.06$  ( $SA_s$ )). Relative to other tested traits, egg shape and mass were 29-34% and 20-25% lower respectively in the percentage of variation that was between-individual in Africa (Table 6.1).

Variation in egg shape and mass, both within clutches and between individuals, did not differ between African populations, or between source and introduced populations (egg shape within-clutch: ANOVA  $F_{3,318}=3.29$ , pairwise  $G_s/SA_s$   $P=0.95$ ,  $SA_s/M_i$   $P=1.0$ ,  $G_s/DR_i$   $P=1.0$ ; egg mass within-clutch:  $F_{3,314}=1.30$ , pairwise  $G_s/SA_s$   $P=0.65$ ,  $SA_s/M_i$   $P=1.0$ ,  $G_s/DR_i$   $P=0.49$ ; egg shape between-individual:  $F_{3,362}=0.96$ , pairwise  $G_s/SA_s$   $P=1.0$ ,  $SA_s/M_i$   $P=1.0$ ,  $G_s/DR_i$   $P=1.0$ ; egg mass between-individual:  $F_{3,374}=2.30$ , pairwise  $G_s/SA_s$   $P=1.0$ ,  $SA_s/M_i$   $P=1.0$ ,  $G_s/DR_i$   $P=1.0$ . See Figs. 6.9, 6.10). The between-individual component for egg mass variation was 6% higher in Mauritius than South Africa, and 9% higher in the Dominican Republic than The Gambia (Table 6.1).

### **Eggshell Color**

Almost all (>96%) of the variation in egg color in the two African populations was between individuals (Table 6.1). Brightness and chroma, as determined from color chart assessments, had the highest between-individual percentage of total variation among the egg appearance variables tested.

Mean egg color variation within a clutch was similar between African populations, as well as between Mauritius and South Africa; but Dominican clutches were more variable than Gambian clutches. This was the case both for brightness (Fig.6.11A; ANOVA:  $F_{3,431}=16.8$ , pairwise  $G_s/SA_s$   $P=1.0$ ;  $SA_s/M_i$   $P=1.0$ ;  $G_s/DR_i$

$P < 0.00001$ ) and chroma (Fig.6.11B; ANOVA:  $F_{3,431}=15.8$ , pairwise  $G_s/SA_s$   $P=1.0$ ;  $SA_s/M_i$   $P=0.38$ ;  $G_s/DR_i$   $P < 0.00001$ ) as assessed by color charts.

Mean egg color variation between individuals were similar between African populations, by both spectral and color chart data (Fig.6.12, 6.13; spectral brightness PC1 ANOVA:  $F_{3,433}=18.5$ , pairwise  $P=1.0$ ; spectral hue/chroma PC2:  $F_{3,431}=7.5$ , pairwise  $P=1.0$ ; chart brightness:  $F_{3,499}=12.1$ , pairwise  $P=1.0$ ; chart chroma:  $F_{3,499}=35.0$ ; pairwise  $P=0.17$ ). Between-individual variation in spectral factor PC3 did not differ across any populations (Fig. 6.13C; ANOVA:  $F_{3,434}=0.07$ ,  $P=0.97$ ). Spectral data show a trend towards lower between-individual variation in brightness in Mauritius than in South Africa (Fig. 6.12B;  $P=0.06$ ), but between-individual variation in brightness as assessed with color charts was not different (Figs.6.12A, 6.14,  $P=1.0$ ). There was no significant difference in between-individual chroma variation between Mauritius and South Africa (Figs. 6.13, 6.14; spectral hue/chroma PC2  $P=1.0$ ; chart chroma  $P=1.0$ ). By both methods, and in both brightness and chroma, Dominican egg color variation between individuals was much lower than Gambian (Figs. 6.12, 6.13, 6.15; spectral brightness PC1  $P < 0.00001$ ; spectral hue/chroma PC2  $P=0.033$ ; chart brightness  $P < 0.00001$ ; chart chroma  $P < 0.00001$ ). The between-individual component of egg color was 23% lower in brightness and 27% lower in chroma in the Dominican Republic than in The Gambia. By a wide margin this difference was the largest found in interpopulation comparisons of traits in this study (Table 6.1).

We also noted when an egg appeared (by our subjective assessment) to be inconsistent in color over its surface, in The Gambia and the Dominican Republic. We noted this for 16 of 177 eggs (9%) in The Gambia, and 59 of 271 eggs (22%) in the

Dominican Republic ( $\chi^2$ :  $P=0.0004$ ). Inconsistency affected 14 of 125 clutches (11%) in The Gambia, and 33 of 164 clutches (20%) in the Dominican Republic ( $\chi^2$ :  $P=0.042$ ). This inconsistency was either mottling, unpigmented spots, or a darker band in one area of the egg.

### **Eggshell Spotting**

In each population, the four spotting variables were within 10% of each other in the degree to which egg spotting variation was between-individual rather than within-clutch. This percentage was 88-92% for South Africa, 78-88% for Mauritius, 93-98% for The Gambia, and 80-88% for Dominican republic (Table 6.1).

Within-clutch disparity in all four egg spotting variables differed among populations in four-way comparisons. The African populations differed, with spot size, density, and aggregation being more variable within South African clutches than within Gambian clutches (Mann-Whitney  $U$  test; spot size:  $U=5346$ ,  $N_G=99$ ,  $N_{SA}=122$ ,  $P=0.011$ ; spot density:  $U=5332$ ,  $N_G=99$ ,  $N_{SA}=122$ ,  $P=0.002$ ; spot aggregation:  $U=5363$ ,  $N_G=99$ ,  $N_{SA}=122$ ,  $P=0.012$ ). Disparity in spot color within a clutch, however, was similar between the African populations ( $U=5820$ ,  $N_G=99$ ,  $N_{SA}=122$ ,  $P=0.37$ ). Spot size disparity within a clutch was similar between South Africa and Mauritius ( $U=3310$ ,  $N_{SA}=122$ ,  $N_M=52$ ,  $P=0.51$ ), but Dominican clutches were more disparate than Gambian clutches in spot size ( $U=9514$ ,  $N_G=99$ ,  $N_{DR}=154$ ,  $P<0.00001$ ). In both spot density and aggregation, the Mauritius population exhibited a trend towards greater within-clutch disparity than the South African population (spot density:  $U=3499$ ,  $N_{SA}=122$ ,  $N_M=52$ ,  $P=0.10$ ; spot aggregation:  $U=3532$ ,  $N_{SA}=122$ ,  $N_M=52$ ,  $P=0.09$ ), and the Dominican population was significantly more disparate than the Gambian (spot density:  $U=9665$ ,

$N_G=99$ ,  $N_{DR}=154$ ,  $P<0.00001$ ; spot aggregation:  $U=9657$ ,  $N_G=99$ ,  $N_{DR}=154$ ,  $P<0.00001$ ).

Both introduced populations had greater within-clutch disparity than their source populations in spot color (SA<sub>s</sub>/M<sub>i</sub>:  $U=3624$ ,  $N_{SA}=122$ ,  $N_M=55$ ,  $P=0.018$ ; G<sub>s</sub>/DR<sub>i</sub>:  $U=8681$ ,  $N_G=99$ ,  $N_{DR}=154$ ,  $P=0.004$ ). These results are similar to those from  $\chi^2$  tests (Table 6.2).

Between-individual variation in spotting variables did not vary within Africa, or between source and introduced populations, in four-way interpopulation comparisons (Kruskal-Wallis test; spot size:  $H_3=4.42$ ,  $P=0.22$ ; spot density:  $H_3=0.89$ ,  $P=0.83$ ; spot color:  $H_3=5.55$ ,  $P=0.14$ ; spot aggregation:  $H_3=2.65$ ,  $P=0.45$ ). In two-way population comparisons spot color was less variable in the Dominican Republic than in The Gambia (Mann-Whitney  $U=8575$ ,  $N_G=125$ ,  $N_{DR}=164$ ,  $P=0.016$ ). There was a trend towards spot size being less variable on Mauritius than in South Africa (Mann-Whitney  $U=3742$ ,  $N_{SA}=128$ ,  $N_M=68$ ,  $P=0.10$ ). The contribution of between-individual variation to total variation in egg spotting variables was 3-12% lower in Mauritius than in South Africa, and was 8-16% lower in the Dominican Republic than in The Gambia (Table 6.1). Comparison of mean disparity values in Table 6.1 shows that these differences are due almost entirely to an increase in within-clutch variation, rather than a decrease in between-individual variation, with the slight exception of spot color between The Gambia and Dominican Republic.

The proportion of the population that laid spotted eggs did not differ between the two African populations, but 16% fewer clutches contained spotted eggs in Mauritius than in South Africa ( $\chi^2$ :  $P=0.028$ ), and 14% fewer clutches contained spotted eggs in the Dominican Republic than in The Gambia ( $\chi^2$ :  $P=0.025$ ).

## **DISCUSSION**

The results of this study meet all four predictions of the hypothesis that village weaver egg appearance is maintained by natural selection primarily as a counteradaptation to interspecific brood parasitism. Egg appearance features used in egg discrimination (egg color and spotting) are the ones that provide the most reliable signature information in the presence of the cuckoo (P1), reliability being determined by within-clutch uniformity and between-clutch diversity. This reliability is lower in populations that have been removed from cuckoo parasitism, after one century on Mauritius (P2) and after two centuries or more in the Dominican Republic (P3). Moreover, the decrease in reliability is greater in the introduced population that has had the longer duration of allopatry with the cuckoo (P4).

### **Egg Appearance Signature Reliability**

In Africa where the diederik cuckoo parasitizes weaver nests, egg color and spotting differ little within a clutch, which facilitates egg recognition by the incubating female; but eggs are highly variable on the population level in these variables, which decreases the probability of a closely matching foreign egg appearing in the nest. Egg shape and mass are less reliable than color or spotting because they differ more within a clutch and less between clutches. These results are consistent with those of Lahti & Lahti (2002) that village weavers reject foreign eggs in proportion to the difference between their own and the foreign eggs in color and spotting, but not in shape and mass (see also Victoria 1972).

### **Egg Appearance Evolution**

Evidence suggests that the observed changes in egg color and spotting between source and introduced populations are not plastic but evolutionary. Egg color and spotting in a female village weaver are consistent throughout her lifetime (Collias 1984; 1993). Moreover, the range of colors of the eggs laid by captive West African village weavers housed in Los Angeles, U.S.A. and fed commercial feed is similar to the range of colors we observed in the eggs of wild Gambian birds (we used the same color atlas; compare Fig.6.18 with Collias (1984)). Studies of other birds likewise show that egg color and spotting do not ordinarily vary widely with environmental (including dietary) factors (Goodman & Shealy 1977; Mikšík et al. 1996). Egg color has been artificially selected during the domestication of poultry, and Punnett's major genetics work was on inheritance of egg color in fowl (Punnett & Bailey 1920). Egg appearance is part of the mother's extended phenotype (in the sense of Dawkins 1982), and is not influenced by her mate or the offspring (Lang & Wells 1987; Gosler et al. 2000). Egg color in fowl appears to be under polygenic autosomal control (Hutt 1949). The first study of the inheritance of egg appearance in a passerine bird concluded that Mendelian expectations are followed in the inheritance of egg background color in captive village weavers (Collias 1993). Recent evidence from great tits (*Parus major*) suggests that egg spotting pattern might be inherited through the female line (Gosler et al. 2000). As has been suggested for cuckoos (Payne in press), the best candidate for maternal inheritance of egg appearance features may be the W chromosome, the sex chromosome of most birds, including weavers, which is found only in females and contains a significant portion that does not recombine with other chromosomes.

The village weavers on Mauritius, after evolving in the absence of the cuckoo for

115 years, lost some percentage (3-13%) of the reliability of each egg color and spotting variable, as judged by the amount of population variation that is between-individual rather than within-clutch (Table 6.1). The only significant single effect difference between Mauritius and South Africa, however, was the increase in within-clutch disparity in spot color. Trends existed towards increases in the within-clutch disparity of spot density and aggregation, as well as decreases in the population-level variability of egg spectral brightness and spot size. The remaining differences in within-clutch and between-individual variation between Mauritius and South Africa, though nonsignificant, were in the predicted direction for egg brightness, chroma, and all spotting variables, the one exception being egg chroma as determined from color charts, its slight change differing from spectral data. The low scale of the differences could be partially due to the small sample sizes in the Mauritian dataset. Nevertheless, viewed as a whole, the results from the Mauritian population indicate evolution in the direction of lower population variability and higher within-clutch variability, to a small but consistent degree across egg appearance characteristics.

Egg appearance also evolved in the Dominican population, during the two centuries or more since being removed from the risk of cuckoo parasitism in West Africa. As predicted, the changes were similar in direction to those between the South African and Mauritian populations, but were greater in magnitude for all variables. Within Dominican clutches, variation in both brightness and chroma of eggs, and all spotting characteristics, increased strongly relative to clutches in The Gambia. Population-level variation decreased considerably in egg brightness and chroma as well, by both methods of assessment, but spotting decreased in variability only in its color. Of 15 measures of

egg color and spotting, 13 changed in the predicted direction, and 11 of those were statistically significant, 8 at the  $p < 0.00001$  level. This translates into a 23% loss in the reliability of brightness, 27% in chroma, and 8-17% in spotting variables, relative to the reliability of those features in the Gambian population. These differences are readily visible to the human eye. Unlike Gambian clutches, for instance, Dominican clutches often varied conspicuously between and even within eggs in the amount of pigment deposited as ground color, although other aspects of the egg color and spotting pattern were the same, indicating that the same female had laid the eggs (see discussion of conspecific brood parasitism, below). On a population level, Dominican eggs were consistently very dark. No white or light-colored eggs were present in the population, unlike the other three populations. In fact, many eggs in the Dominican Republic were darker than any eggs observed in any other population (see interpretation of these changes below).

### **Unpredicted Egg Size and Spotting Differences**

Two sources of variation among populations, though not contrary to predictions, were nevertheless not predicted. The first is the (statistically nonsignificant) difference in egg mass between source and introduced populations: within-clutch variability was higher and between-clutch variability lower, in both introduced populations relative to their source populations; and to a greater extent in the older introduced population than the more recently introduced one. These differences could be biologically irrelevant, but (1) all four slight differences were in the directions that would be expected if egg mass were an egg signature in Africa (P2 and P3: see Introduction), (2) the changes were greater after a longer divergence from the parental population (P4), (3) the African

populations were similar to each other in these respects, and (4) egg shape had no such differences.

Some other birds use egg size to recognize their eggs (Rothstein 1982; Marchetti 2000). Moreover, Friedmann (1968) suggested that diderik cuckoo egg size may have evolved in response to weavers, because diderik eggs laid in village weaver nests were larger than diderik eggs found in the nests of two other, smaller-egged *Ploceus* species. His observation is consistent with egg recognition on the basis of size, but diderik cuckoo egg size might also have evolved to match weaver egg size for the sake of incubation efficiency. If cuckoo eggs were occasionally larger or smaller than village weaver eggs generally are, weavers could use egg size as a species-wide signature without having the finer signature reliability that color and spotting possess. The diderik cuckoo egg size range is very close to the range of weaver eggs, however, although some diderik eggs (not necessarily from village weaver nests) are smaller than village weaver eggs (James 1970; Priest & Winterbottom 1971; Maclean 1993). Perhaps egg size or mass is used to a small degree by weavers in egg discrimination, but its effects are masked by those of color and spotting.

Another unpredicted result is that significantly fewer eggs in introduced populations are spotted, than in their source populations. Eggs of village weavers in Africa are spotted in 74-78% of clutches, but this declined to 58% on Mauritius and 64% in the Dominican Republic. This raises the interesting possibility that egg spotting itself, as distinct from variation in spotting, may be an adaptation to avoid brood parasitism. Since spotting is consistent within an individual, weavers that lay spotted eggs increase the complexity of their egg signature, and make mimicry more difficult for a cuckoo.

The minority proportion of the parasitized populations that continue to lay plain eggs meets the expectation of frequency-dependent selection: as long as most weavers are laying spotted eggs, most cuckoos should as well, so plain weaver eggs will be distinctive and will permit easy discrimination against most cuckoo eggs. Moreover, apparently no evidence exists for any function for egg spotting besides parasitic mimicry, crypsis, and egg recognition (Underwood & Sealy 2002), although many species' eggs are spotted for unknown reasons. Since village weavers lay eggs in enclosed nests, they may not benefit from spotting their eggs in the absence of the cuckoo. Lack of selection may thus have led to a decline in spotted eggs in the introduced populations.

### **Functions of Egg Variability and Clutch Uniformity**

This study substantiates predictions from the hypothesis that bird clutch uniformity is maintained by natural selection for egg recognition (Davies & Brooke 1989b). In fact, egg recognition is the only function that has been demonstrated for bird clutch uniformity per se, as distinct from uniformity being a byproduct of selection for another function such as crypsis. No data are available as to whether the degree of uniformity in the parasitized populations of the village weaver is unusual among birds.

Evidence has been adduced for only two functions of polymorphism in egg appearance: egg recognition (Tschanz 1959; Victoria 1972; Moksnes 1992; this study), and mimicry of host eggs by brood parasites (Baker 1942; Payne 1967; Davies 2000). Most bird species, on the other hand, lay eggs that are relatively invariant within a species. Although no quantitative comparative study has yet been performed, the level of population variability found in village weavers is extreme among birds (Moreau 1960; Schönwetter 1983; Freeman 1988) and is probably only approached by that of cuckoos

that parasitize a variety of hosts, such as the common cuckoo *Cuculus canorus* (Davies 2000).

The question remains as to why weavers have such polymorphic eggs while other species also subject to brood parasitism do not display such variation. Rothstein and Robinson (1998) proposed an explanation based on the unique nest structure of weavers. In most open-nesting birds subject to parasitism, selection for egg appearance is exerted not only by parasites but also by predators (and, one might add, perhaps solar radiation (Bakken et al. 1978; Underwood & Sealy 2002)). Egg polymorphism may therefore be constrained for the need for eggs to be cryptic (and cool?). In most hole-nesting birds, on the other hand, so little light enters the brood chamber that egg polymorphism in appearance would not be functional even if the species were subject to brood parasitism. Weavers have an enclosed nest that is too opaque for crypsis to be necessary, but is translucent enough for egg discrimination to be possible (Lahti & Lahti 2002), permitting the evolution of an adaptive polymorphism.

### **Two Alternative Hypotheses for the Evolution of Egg Appearance**

Moreau (1964) thought that the broad population-level variability in weaver egg appearance could be explained solely by the absence of stabilizing selection by nest predators, due to the enclosed nature of weaver nests. Under this hypothesis, variability is seen as a result of neutral evolutionary processes. Swynnerton (1916) also mentioned this possibility. This hypothesis implies that multiple alleles have persisted indefinitely in a population and have even tended to proliferate, each allele contributing to a different phenotype, all of which have equivalent (or no) functionality. The hypothesis also implies that a broad variety of physiological recipes for pigment production and

deposition do not differ in cost among themselves to an extent that would be relevant to natural selection over evolutionary time. The present study indicates, on the other hand, that brood parasitism maintains weaver egg color polymorphism, as Bates (1911) suggested, and that in the absence of such selection the multiplicity of alleles does not persist indefinitely in a population.

Egg polymorphism in weavers has also been suggested to be maintained by conspecific brood parasitism (Freeman 1988; Jackson 1992a; 1992b; 1998), contrary to the conventional perspective that egg-mimicking cuckoos are the source of selection (Cruz & Wiley 1989; Rothstein 1990; Rothstein & Robinson 1998; Payne 1998).

Observations of the rarity of conspecific brood parasitism in wild and captive village weavers have led Victoria (1972) and the Colliases (Collias 1993; Collias & Collias 1998) to conclude that cuckoo parasitism was the agent of selection. No rigorous test of conspecific parasitism has been performed in this species, however. The present study meets predictions from the hypothesis of selection from cuckoos, and falsifies the hypothesis of conspecific parasitism as the predominant source of selection.

Counteradaptations to conspecific brood parasitism would not be predicted to decline in introduced populations. I know of no reason to suppose that conspecific brood parasitism frequency has declined drastically in the introduced populations of the village weaver.

Before this study, however, researchers have noted problems with the idea that egg recognition and egg polymorphism could evolve in weavers if the predominant source of selection were conspecifics (Rothstein and Robinson 1998: 40). Even if village weavers have been parasitized both by conspecifics and cuckoos, one might expect conspecific brood parasitism to exert far weaker selection for defenses, for two reasons. (1)

Conspecific brood parasitism does not usually nullify the reproductive attempt of the host, because young do not evict nestmates and parasites might not remove eggs; and (2) parasitic individuals are also susceptible to parasitism themselves, so individual costs and benefits of parasitism may cancel each other out to some extent.

### **What Has Been the Mechanism for the Evolution of Egg Appearance in Allopatry?**

#### *Increase in within-clutch variation*

Within-clutch variation increased in populations of the village weaver that have been removed from parasitism by the diderik cuckoo. This evolution could be the result of relaxation of selection on physiological precision in egg pigment production and deposition. The best supported hypothesis for the variation in egg appearance within a clutch found in many birds (typically due to an odd last egg) is the female running out of pigment before clutch completion (Underwood & Sealy 2002). Physiological studies have shown that egg colors and spots are not deposited randomly by free masses of pigment, but are produced by specialized pigment cells in the epithelium of a bird's shell gland, which release pigment in an orderly, timed manner (Poole 1967). The precision of this order and timing, and of the pigment supply, apparently differs among species, and high precision might bear a cost. When clutch disparity impacts fitness in the context of brood parasitism, individuals benefit by expending that extra cost to keep even the last egg consistent. The maintenance of similarity within a clutch in the presence of cuckoo parasitism, therefore, could be analogous to the precision that is thought to be required for bodily symmetry (Møller & Thornhill 1998). To the extent that the cuckoo is the source of selection on weaver egg appearance, precision in pigmentation of eggs would be unnecessary in the introduced populations. The rapidity of the decline in uniformity

may be the result of direct selection against this nonfunctional refining mechanism in the introduced populations due to energetic costs. Alternatively, the loss of uniformity could be a byproduct of selection on genetically or phenotypically correlated traits.

*Decrease in egg polymorphism: founder effect and genetic drift*

Egg variability between village weaver individuals decreased in the populations in allopatry with the diederik cuckoo. Hypothesizing a mechanism for this evolutionary change is complex. Unlike the increase in clutch variability, the decline in egg polymorphism is predicted by the founder principle (Mayr 1942). The founder effect as an explanation is not really an alternative to natural selection, however (Berry 1998). A founder effect can be considered as a founding event (a decrease in genetic variability compared to the source population) plus subsequent founder selection, or natural selection within the smaller founding population. Founder selection may be more intense because of the smaller effective population size and the shifts in gene frequencies usually associated with a founding event (Mayr 1963; Halkka et al. 1974). Population bottlenecks have been observed to facilitate rapid adaptive evolutionary change in Darwin's finches (Boag & Grant 1981) and *Spartina* cordgrass (Daehler & Strong 1997), and island colonizations often result in a decrease in genetic variability as well as local adaptation (e.g., Berry 1964). Genetic drift might also contribute to evolution after the founder event, but this has not received empirical support (Berry 1998).

An investigation into the mechanism of decline in egg polymorphism should therefore involve the assessment of the relative contribution of three factors: (1) bias due to characteristics of the introduced individuals, (2) genetic drift, and (3) natural selection. Without knowledge of the genetic structure of the populations, such assessment can only

be preliminary. In the case of the decline of polymorphism in the Dominican Republic, characteristics of the founders may have played some role, as preliminary evidence from RAPD markers suggests that Dominican weavers are less genetically diverse than their source population in Africa (Lahti, unpublished data). Four considerations, however, suggest that the role of this factor is not overwhelming. First, changes in several traits have occurred, all of which are predicted by the hypothesis of shift in selective regime, whereas changes in some of these traits, such as increase in within-clutch variability, are not as readily explicable in terms of a decrease in genetic diversity without *ad hoc* assumptions. Second, changes in the same specific traits, and in the same direction, including decline in polymorphism, occurred both on Mauritius and in the Dominican Republic. The founder event hypothesis therefore requires the unlikely scenario that the chance collection of phenotypes in both founding populations shared distinctive features. Third, the distribution of egg polymorphism in Africa is such that a random sample of individuals from a single locality will contain a broad variety of egg morphs. Even small colonies (<15 nests) have nearly the diversity in egg appearance of much larger colonies (Fig.6.16). This suggests that even a small founding propagule might have contained nearly the entire range of African egg appearance variability. Fourth, introductions to Hispaniola appear to have been several over an extended time period, whereas the Mauritian birds descend from a single introduction of a few individuals. Introductions to Hispaniola, moreover, appear to have ceased over two centuries ago, whereas the Mauritian introduction occurred more recently. On the basis of these facts, one would predict that a founder event would be more evident on Mauritius than in the Dominican Republic. On the contrary, the evidence indicates a small degree of change on Mauritius,

and a much larger degree of change on Hispaniola, relative to their source populations.

Some of the considerations that decrease the estimated contribution of a founder event (the first, second, and fourth above) also decrease the likelihood of genetic drift as an explanation for the observed changes.

*Decrease in egg polymorphism: natural selection*

The loss of egg color polymorphism in the Dominican Republic suggests that the alleles with the largest effects on egg appearance appear to have become fixed there, since so many African egg morphs are absent from the island population, and existing variation in egg color is small (Fig.6.15). Moreover, certain alleles or allelic combinations are abundant in the Dominican population despite being absent from the source population. The Dominican birds exhibit a restricted range of egg colors, including eggs darker than any eggs I have seen in Africa (Fig.6.15). Thus, whatever mechanism accounts for the evolution of egg appearance in this lineage in the last 200 years must account for two observations: (1) rapid phenotypic homogenization, and (2) directional phenotypic change. Such a mechanism might also explain (3) the more rapid evolution of color than spotting. Founder effect predicts the first observation only. Genetic drift does not predict any of these observations specifically. *Ad hoc* drift explanations are always possible; for example, a mutation similar in effect to that which produces the "sepia" *Drosophila* due to an overaccumulation of pigment (Prout 1964), could have originated and drifted to abundance when the effective population size was very small. If natural selection were involved in the loss of population variability in egg color, it might be indirect, in which case an ignorance of the relevant genetic and phenotypic correlations precludes prediction. If direct, selection might simply have

resulted in the loss of those pigment combinations that bear some physiological cost relative to the subset that has persisted. Ignorance of relative costs of the physiological process of pigment production and deposition likewise precludes prediction here. What remains is the possibility of direct selection on the persisting subset of egg appearance phenotypes.

I propose natural selection for the reduction of solar heating and mutagenesis in the developing embryo, as the mechanism for the loss of polymorphism in egg appearance in Dominican weavers. This hypothesis can explain the Dominican population's phenotypic homogenization, directional change, and greater rapidity of evolution of color than of spotting. Village weavers in the absence of selection for reliable egg signature information, may have responded to selection for an egg color that maximizes embryonic survival in the natural light environment of the egg. In order to describe this hypothesis fully, it must be placed into the context of a general theory of egg pigmentation.

### **Egg Color as an Adaptation to Solar Radiation**

Embryos are sensitive to increases in temperature (Romanoff 1960). Avian eggshells reflect very strongly in the near-infrared (IR), where nearly half of incident solar energy occurs (Bakken et al. 1978), which raises the possibility that bird eggs may be adapted to solar heating or mutagenesis. In sunlight, naturally white eggs painted tan experienced an increase in temperature relative to unpainted eggs, exceeding lethal embryonic limits (Montevecchi 1976). Painting ostrich (*Struthio camelus*) eggs brown increases mortality due to heat (Bertram & Burger 1981) while decreasing vulnerability to predators. In a situation of weak or absent selection for cryptic or polymorphic eggs,

then, birds with eggs exposed to sunlight might respond to selection among varying rates of embryonic survival due to solar heating or mutagenesis.

Evidence from studies of experimentally painted eggs, and the understanding that white eggshells reflect a high proportion of light across the spectrum, have commonly led to the prediction that eggs subject to selection by sunlight should be white unless crypsis, egg recognition, or some other source of selection is stronger. Blue to blue-green eggs, however, are common among arboreal open-cup nesters, although the function is unclear (Lack 1958; Underwood & Sealy 2002). Egg recognition has not been supported as a function (Lorenzana & Sealy 2002), nor has crypsis (reviewed by Underwood & Sealy 2002), although painting eggs is of doubtful utility in such studies. Bakken et al. (1978) demonstrated that the blue eggs of arboreal nesters have high reflectance in the near-IR, and that this high reflectance is not the case in the typical blues that vertebrates produce. This highlights the possibility that solar radiation is a threat to the survival of these eggs despite their shaded environment. However, high near-IR reflectance can also be produced in a white egg; so why some exposed eggs are pigmented at all in the human visible range remains unexplained (Bakken et al. 1978).

Any incident light that is not reflected from a surface is either absorbed by the surface or transmitted through it. These three values are proportional and exhaustive. In most studies of color in biology, reflectance values are used (Endler 1990; Endler 1993; Bennett et al. 1997). For consideration of the effects of solar heating and mutagenesis, the proportion of unreflected light that is transmitted versus absorbed is also of interest. Even a white egg does not reflect all light, and the remainder may damage the embryo if it transmits through the shell. Eggshell thickening would decrease transmission, but

might also prevent the young bird from being able to hatch. When considering the value of preventing light from transmitting into an egg, therefore, pigment may be adaptive. A pigmented shell reflects light at fewer wavelengths than a white shell, but absorbs more unreflected light instead of allowing it to transmit. Light absorbed by the shell, however, is converted to heat. Heat in the shell will dissipate to the environment by convection as long as it does not build up too quickly, in which case it will spread to the interior of the egg by conduction.

Two observations in a recent poultry study (Shafey et al. 2002) are illustrative. First, near-UV wavelengths are especially well absorbed by chicken eggshells, rather than transmitting through them to the interior of the egg. This suggests that absorbance may function in the reduction of solar heating or mutagenesis. Second, naturally brown chicken eggs absorb more (transmit less) light than white eggs. The biologically relevant issue in eggshell pigmentation, therefore, is not what color reflects proportionally highest at all wavelengths (white), but what color minimizes the damaging effects of light, by any mechanism.

Solar damage to embryos thus comes from two sources, light transmittance into the egg, and conduction of heat from light absorbed by the shell surface. I hypothesize that these factors are involved in a tradeoff that is mediated by the intensity of the egg's light environment (Fig.6.17). As the light environment increases in intensity, the detriment to embryo fitness increases. I propose that the shape of this function depends on egg pigmentation, such that predictions for optimal egg pigmentation differ in different light environments.

One prediction of this hypothesis is that in high light conditions, eggs should be

white, because any pigment causes the egg to heat up and conduct heat into the interior. The rate of heat dissipation to the environment by convection in intense light is exceeded by the heat buildup in the shell due to the absorbance of light. Absorbance must therefore be minimized in such conditions, and transmittance can only be reduced through reflectance, so eggs should be white or nearly so. In less intense light environments, however, the heat created by light absorption by a pigmented shell accumulates at a low enough rate to be lost by convection. Pigment is adaptive in this situation because it shades the embryo by absorbing light that would otherwise transmit into the egg. In such an environment a pigmented egg keeps an embryo safer from solar radiation than a white egg would. The point of increasing light intensity at which a certain amount of pigment ceases being optimal is the intensity at which heat builds up in the shell at a higher rate than convection can disperse it. If this hypothesis is correct, arboreal birds that lay eggs in environments of low light intensity, should lay pigmented eggs, and the degree of pigmentation should be negatively correlated with typical nest site light intensity among species.

The question remains as to why the pigment of arboreal birds tends to be blue to blue-green. Incident light on eggs in the nests of many arboreal birds have an irradiance (ambient light) spectrum somewhere between that of a bright woodland shade, where most light is filtered through green leaves but some penetrates through small light gaps in the canopy, and a darker forest shade, where nearly all light is filtered through green leaves. Endler (1993) measured the spectral characteristics of such conditions, and concluded that ambient light in bright woodland is bluish, and in denser forest is greenish. Ambient light contains the wavelengths that are likely to be incident on, and

therefore transmit into and heat, an egg. If the above considerations are correct, arboreal birds should have eggs that are pigmented to reflect these wavelengths, i.e. blue-green pigment. The pigment reflects some of the incident light and absorbs a significant proportion of the remainder; and the associated heat is lost to the environment from the shell, minimizing solar heating and mutagenesis of the embryo. An unpigmented (white) egg would also reflect at the blue-green wavelengths, but because it was unpigmented would allow more of the unreflected light to transmit through the shell. An egg of some other color such as brown would absorb well, but perhaps too well (leading to heat buildup), and it would be suboptimal in reflectance at incident wavelengths.

If fitness is affected by light damage at the embryo stage, birds with eggs exposed to sunlight are under selection to minimize damage to the embryo. One way to protect the embryo is to regulate the light and heat regime via egg pigmentation. In many cases, other factors relevant to egg appearance impinge more seriously on fitness, and eggs evolve in another direction. For instance, visually acute nest predators exert selection for eggs to reflect light in a manner similar to their backgrounds. Brood-parasitic egg mimics, as implicated in this study, exert selection for distinctive egg appearance, which can lead to polymorphism. When such sources of selection are weak enough relative to selection by the sun, however, exposed eggs can adapt to the effects of light. When those effects decrease fitness (for they might increase it in some environments), adaptation involves maximizing the cumulative protective effects of light reflectance and absorbance, and minimizing the cumulative detrimental effects of heat conduction and light transmittance. How these values interact depends on the nature of the light environment at the nest site. This hypothesis can be tested in interspecific comparisons,

for instance among open-cup nesters whose nest sites are characterized by differing ambient light spectra and predation regimes.

Applying this general hypothesis to the village weaver can explain the loss of egg variability and the directional evolution of darker blue-green eggs in the Dominican Republic. Although enclosed, the nests of weavers are translucent. Predators would not be able to see through the weave, but sunlight does enter, as evidenced by village weavers' refined egg recognition in Africa (Lahti & Lahti 2002). In many parts of their range, we observed that village weaver nests are commonly exposed to direct sunlight throughout the day due to their tendency to nest in isolated trees and to denude the vegetation around their nests (probably for predator avoidance and mate attraction functions (Collias & Collias 1959; 1969; 1970)). Village weaver eggs may therefore be subject to embryonic damage due to solar radiation.

In Africa, in the presence of the egg-mimicking diderik cuckoo, selection for individually distinctive egg colors for the sake of recognition overrides any selection by solar radiation. In the absence of parasitism, however, such as in the Dominican Republic, weavers may be free to respond to selection for an egg color that maximizes embryonic survival in their eggs' natural light environment. The Dominican weavers may be evolving an eggshell color that most efficiently prevents light from either transmitting to the embryo or heating it up through conduction from the shell.

Village weaver eggs are translucent, especially during the early days of development; in this species one can determine the age of an embryo by holding an egg up to the sun and looking at the embryonic silhouette (Lahti & Lahti 2002). This method could not be used on darker weaver eggs, such as many in the Dominican Republic,

because they were more opaque (Figs.6.3, 6.15). Female village weavers generally lay eggs when the nests are still green (Jacobs et al. 1978). Considering the translucence of weaver nesting materials, the light environment of the nest's interior is probably similar to a woodland shade as described by Endler (1993). Optimal weaver egg coloration in such an environment would be a medium blue-green according to the hypothesis presented above. Dominican weaver eggs may therefore be blue-green because this pigment most effectively prevents incident light from transmitting to the embryo.

### **Conclusion**

Darwin observed the functionality of traits and mentioned, "With both varieties and species, use and disuse seem to have produced a considerable effect." (Darwin 1859: ch.15). Egg polymorphism and clutch uniformity in the village weaver have evolved by natural selection imposed by interspecific brood parasitism, an effect which has been fostered by considerable "use", as these traits permit village weavers to increase the success of their reproductive attempts. "Disuse" of these traits in the absence of parasitism has had a considerable effect as well, in a period of time that may be surprising only because of our ignorance of the mechanisms underlying trait change in this situation. When traits such as egg distinctiveness and clutch uniformity fall into disuse, however, natural selection may operate in another direction, resulting in the evolution of a trait, such as a particular egg color, according to its own "use" in the new ecological context.

Egg Appearance Trait	Source of Variability	South Africa		Mauritius		The Gambia		Dominican Rep.	
		Mean Disparity (Pop. Variance)	% BI						
Shape	WC	0.053 (0.002)	62	0.061 (0.002)	63	0.044 (0.002)	66	0.040 (0.001)	68
	BI	0.086 (0.006)		0.103 (0.005)		0.086 (0.004)		0.084 (0.004)	
Mass	WC	0.160 (0.019)	72	0.177 (0.016)	66	0.124 (0.010)	74	0.164 (0.028)	65
	BI	0.404 (0.114)		0.349 (0.074)		0.357 (0.056)		0.308 (0.069)	
Brightness	WC	0.074 (0.135)	97	0.154 (0.250)	93	0.047 (0.045)	98	0.429 (0.482)	75
	BI	2.188 (2.626)		2.000 (2.716)		2.056 (2.80)		1.256 (1.124)	
Chroma	WC	0.082 (0.142)	97	0.250 (0.623)	93	0.047 (0.064)	99	0.455 (0.472)	72
	BI	2.859 (5.523)		3.147 (6.157)		3.413 (6.117)		1.171 (1.050)	
Spot Size	WC	0.131 (0.094)	89	0.144 (0.082)	86	0.086 (0.163)	93	0.218 (0.137)	84
	BI	1.039 (0.585)		0.868 (0.661)		1.089 (0.766)		1.122 (0.767)	
Spot Density	WC	0.111 (0.093)	92	0.173 (0.136)	88	0.030 (0.050)	98	0.240 (0.252)	85
	BI	1.297 (1.391)		1.324 (0.924)		1.336 (1.382)		1.409 (1.562)	
Spot Color	WC	0.098 (0.089)	92	0.288 (0.347)	80	0.056 (0.040)	96	0.146 (0.091)	88
	BI	1.164 (0.804)		1.147 (1.060)		1.320 (0.816)		1.067 (0.732)	
Spot Aggregation	WC	0.152 (0.165)	88	0.356 (0.523)	78	0.051 (0.059)	96	0.286 (0.238)	80
	BI	1.086 (0.678)		1.265 (0.929)		1.256 (0.853)		1.137 (0.884)	

Mean Disparity is the mean range between two eggs in the population, either within a clutch (WC) or between individuals (BI), for the given egg appearance trait. Pop. Variance (in parentheses) is the variance around this mean. % BI is the percentage of the total mean disparity attributed to between-individual variation. It is a relative indicator of the reliability of the trait as a signature, since an increase in BI relative to WC means increased clutch uniformity and egg distinctiveness. The Gambia and South Africa are the source populations, and Mauritius and Dominican Republic are the respective introduced populations.

**Table 6.1. Sources of Variation in Egg Appearance in the Village Weaver**

Populations compared	Spotting variable		Observed <sup>a</sup>		Expected <sup>a</sup>		N	$\chi^2 P$	Interpretation			
			Same	Diff.	Same	Diff.						
<b>The Gambia vs. South Africa</b>	size	<b>G</b>	93	6	86	13	99	0.008	SA>G			
		<b>SA</b>	100	22	107	15	122					
	density	<b>G</b>	97	2	90	9	99	0.002	SA>G			
		<b>SA</b>	105	17	112	10	122					
		color	<b>G</b>	91	8	89	10			99	0.4	G=SA
			<b>SA</b>	108	14	110	12			122		
aggregation	<b>G</b>	93	6	87	12	99	0.01	SA>G				
	<b>SA</b>	101	21	107	15	122						
<b>South Africa vs. Mauritius</b>	size	<b>SA</b>	100	22	98	24	122	0.4	SA=M			
		<b>M</b>	40	12	42	10	52					
	density	<b>SA</b>	105	17	101	21	122	0.077	M>=SA			
		<b>M</b>	39	13	43	9	52					
		color	<b>SA</b>	108	14	103	19			122	0.02	M>SA
			<b>M</b>	39	13	44	8			52		
aggregation	<b>SA</b>	101	21	97	25	122	0.14	M>=SA <sup>b</sup>				
	<b>M</b>	38	14	42	10	52						
<b>The Gambia vs. Dominican Republic</b>	size	<b>G</b>	93	6	78	22	99	<0.00001	DR>G			
		<b>DR</b>	106	49	121	33	154					
	density	<b>G</b>	97	2	81	18	99	<0.00001	DR>G			
		<b>DR</b>	109	45	125	29	154					
		color	<b>G</b>	91	8	83	16			99	0.004	DR>G
			<b>DR</b>	120	34	128	26			154		
aggregation	<b>G</b>	93	6	76	23	99	<0.00001	DR>G				
	<b>DR</b>	102	52	119	35	154						

<sup>a</sup>From  $\chi^2$  test for independence. Numbers under "Same" refer to the numbers of clutches sampled from that population whose eggs were all placed in the same spotting variable category. Numbers under "Diff." refer to clutches in which at least one egg differed from the others in the relevant spotting variable.

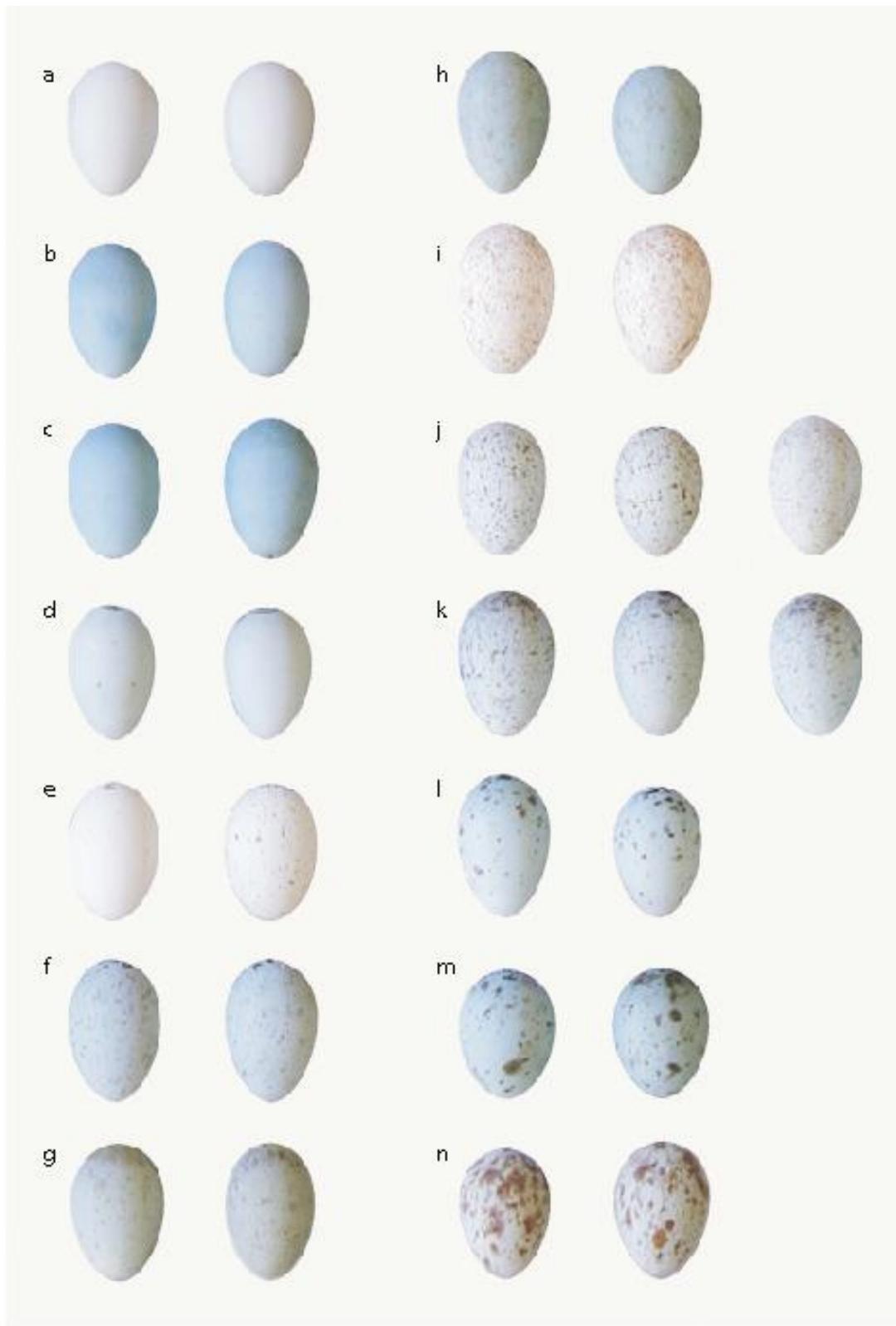
<sup>b</sup>Trend found with Mann-Whitney *U* test (see text).

**Table 6.2. Comparison of Within-Clutch Variation in Egg Spotting Among Populations of the Village Weaver**

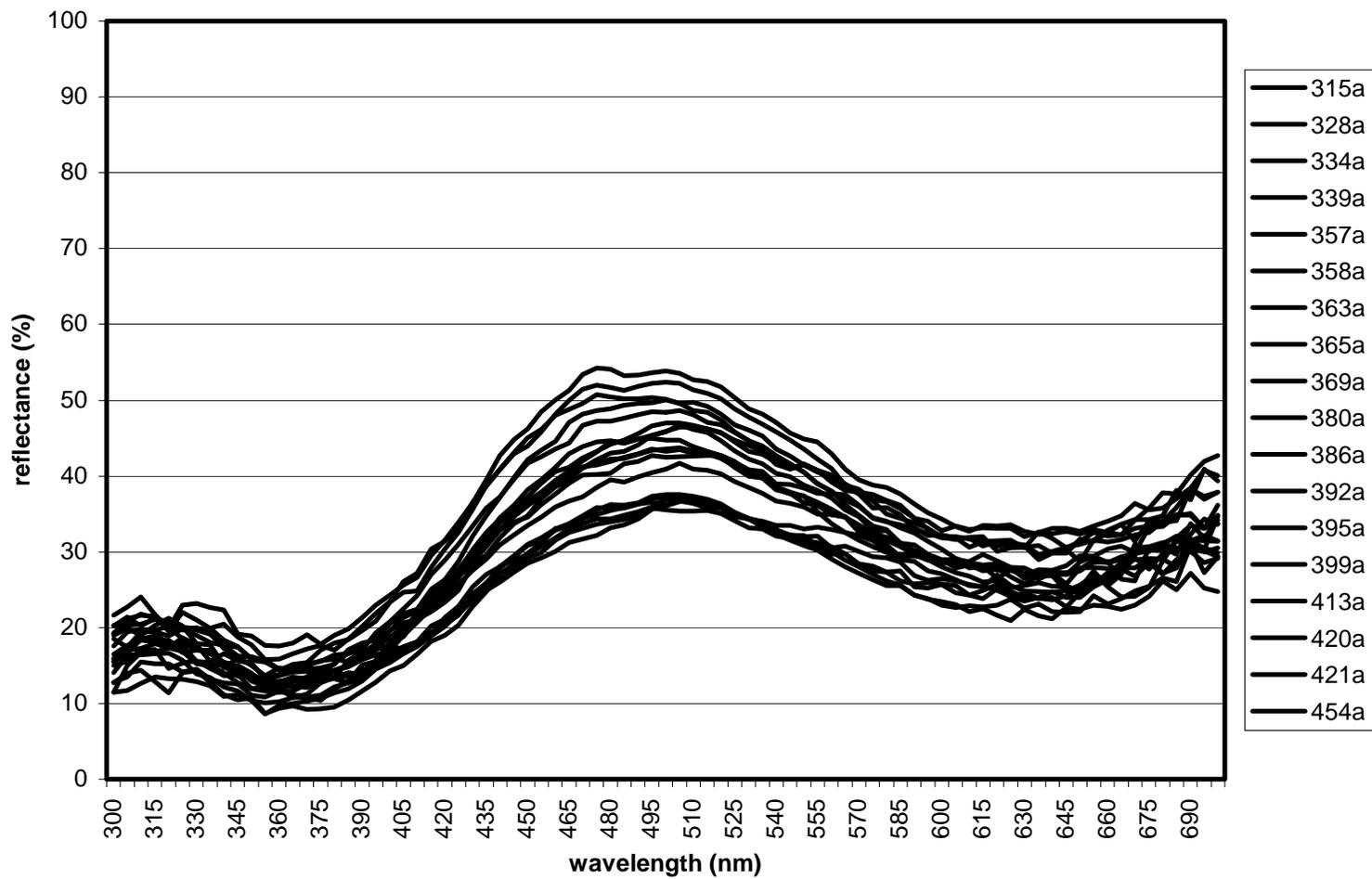


DR<sub>i</sub>=Dominican Republic, G<sub>s</sub>=The Gambia, SA<sub>s</sub>=South Africa, M<sub>i</sub>=Mauritius. Yellow is the natural range, red the introduced range

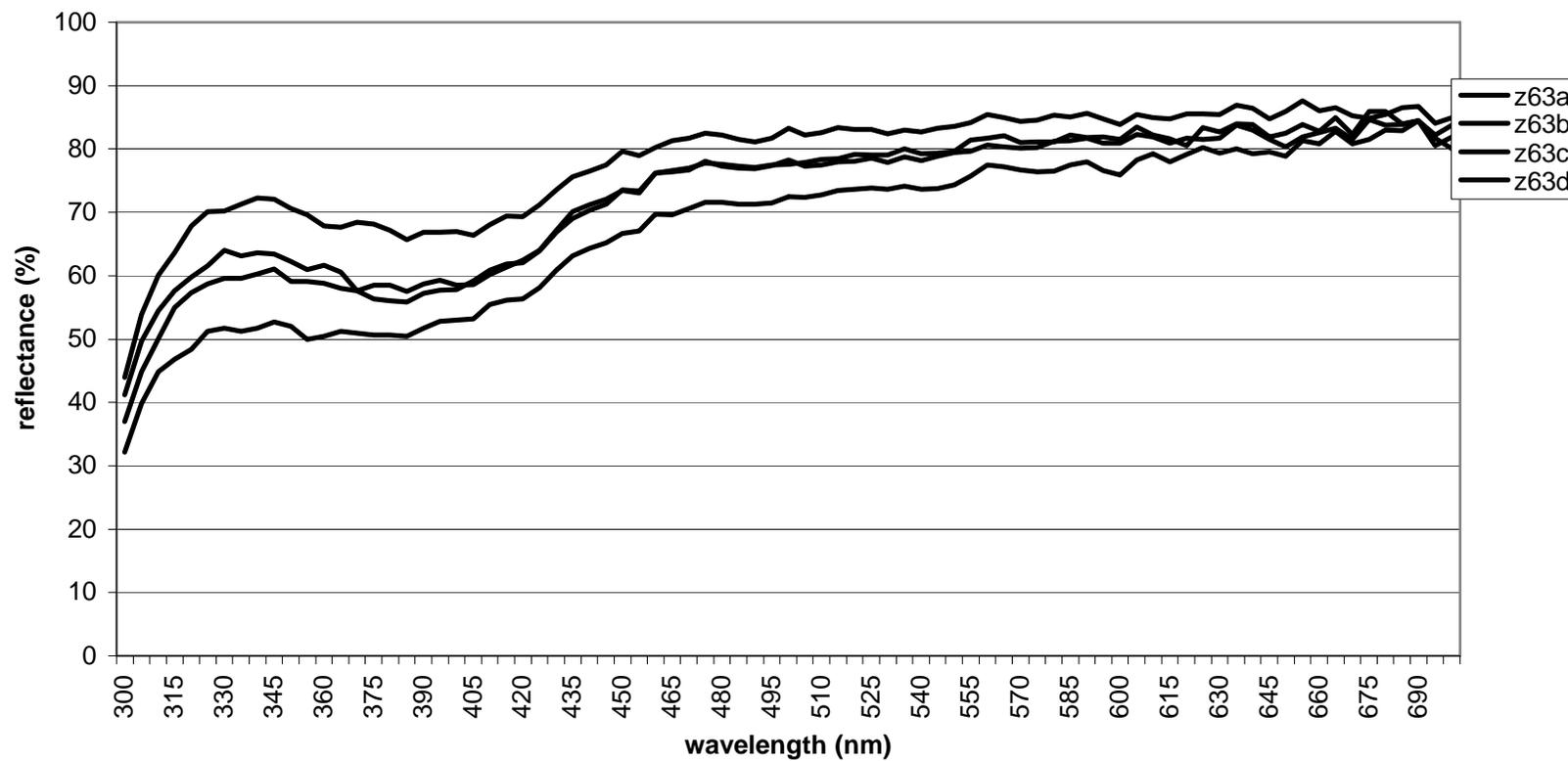
**Fig.6.1. Geographic Range of the Village Weaver (*Ploceus cucullatus*).**



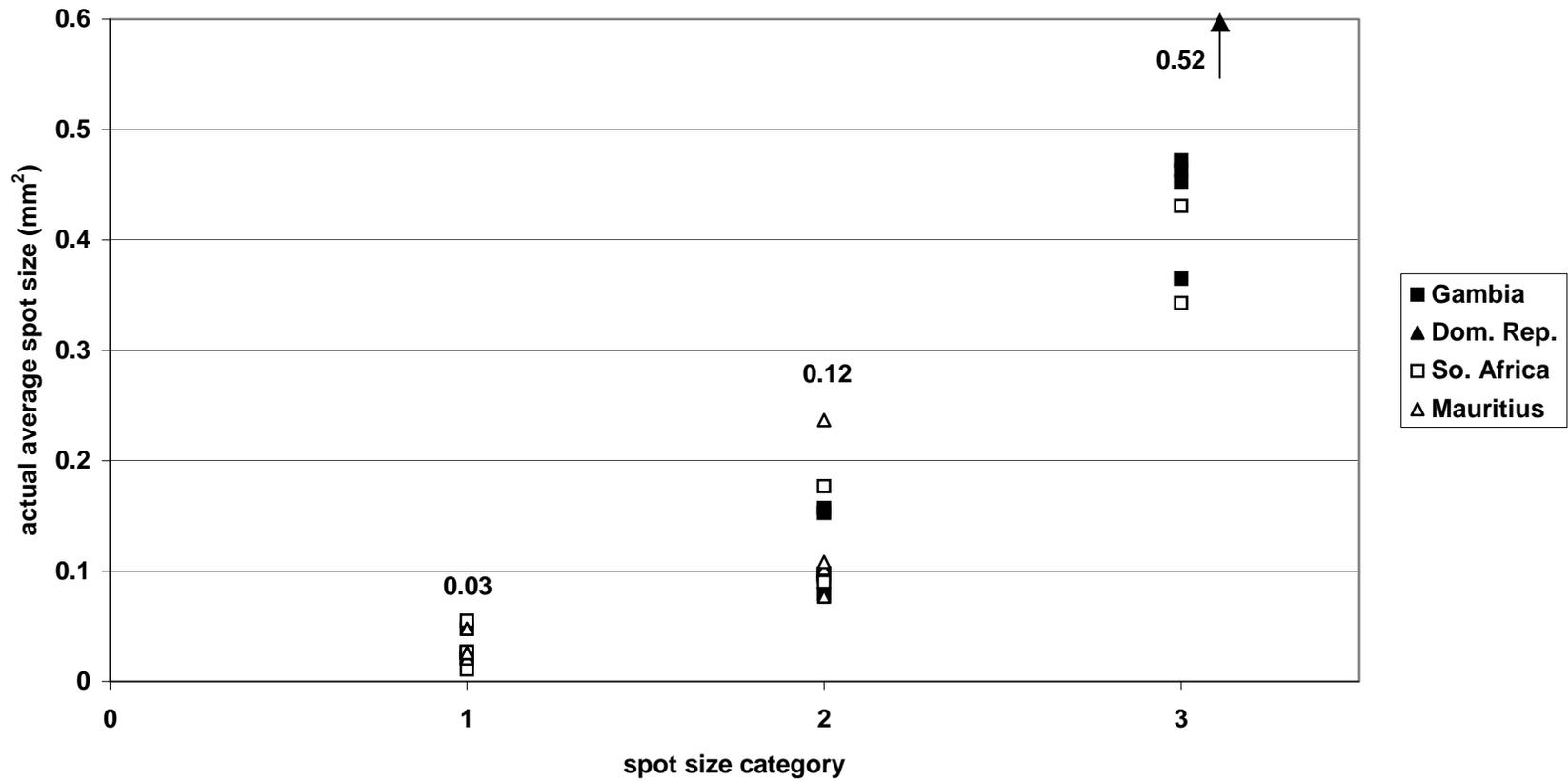
**Fig.6.2. Fourteen Complete Clutches (a-n) of Village Weaver (*Ploceus cucullatus*) Eggs, from Janjangbureh Island, The Gambia (Actual Size)**



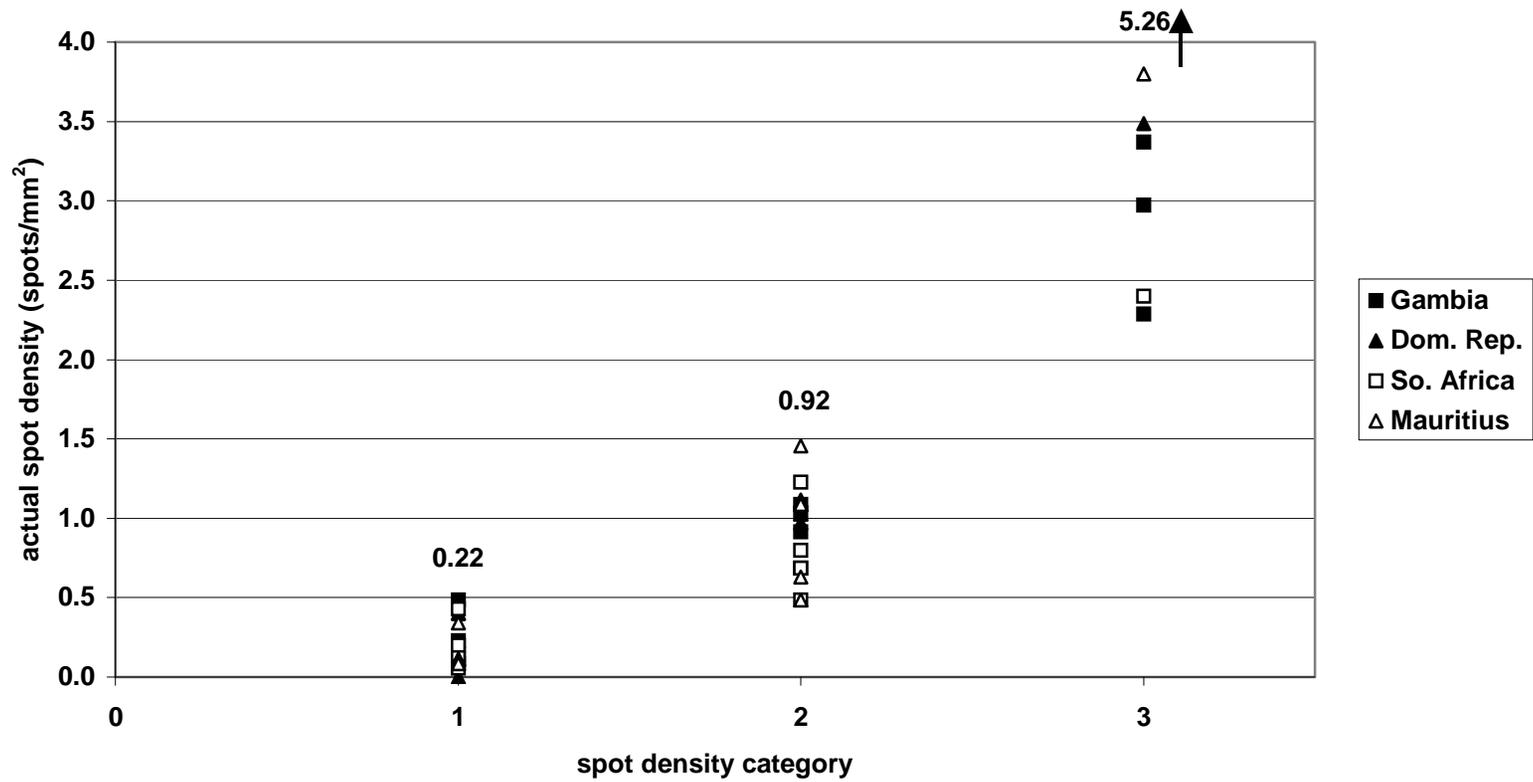
**Fig.6.3. Spectra of 18 Eggs in Different Clutches of the Village Weaver, Dominican Republic (all eggs scored as E 12/6, a medium blue-green, on *Villalobos Color Atlas* (Villalobos 1947))**



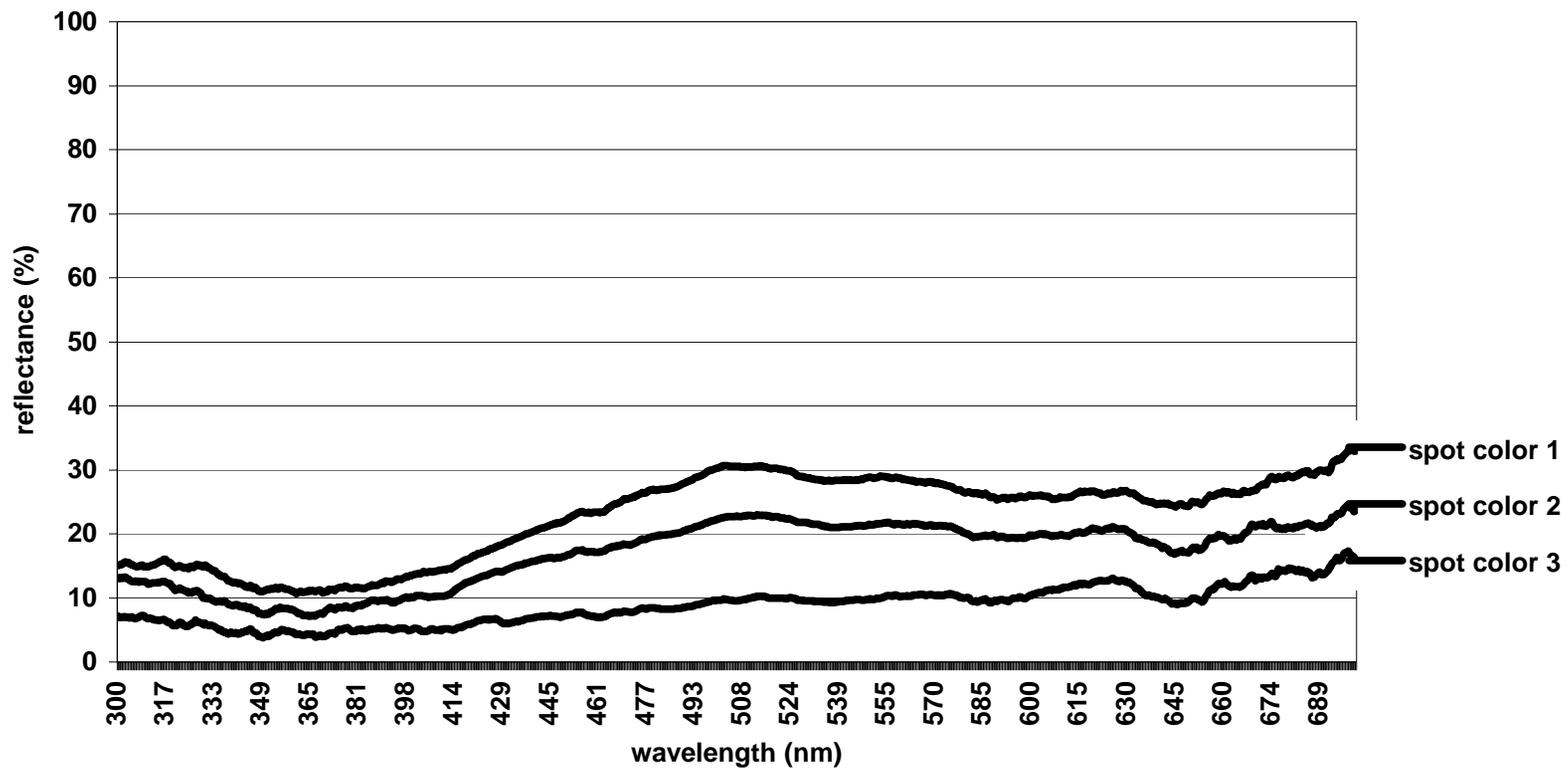
**Fig.6.4. Spectra of a 4-Egg Clutch of a Village Weaver, South Africa**  
**(all eggs scored as E 19/0, white, on *Villalobos Color Atlas* (Villalobos 1947))**



**Fig.6.5. Spot Size in Village Weaver Eggs: Relation of Quantitative Measurements to Index Categories (means above each column)**

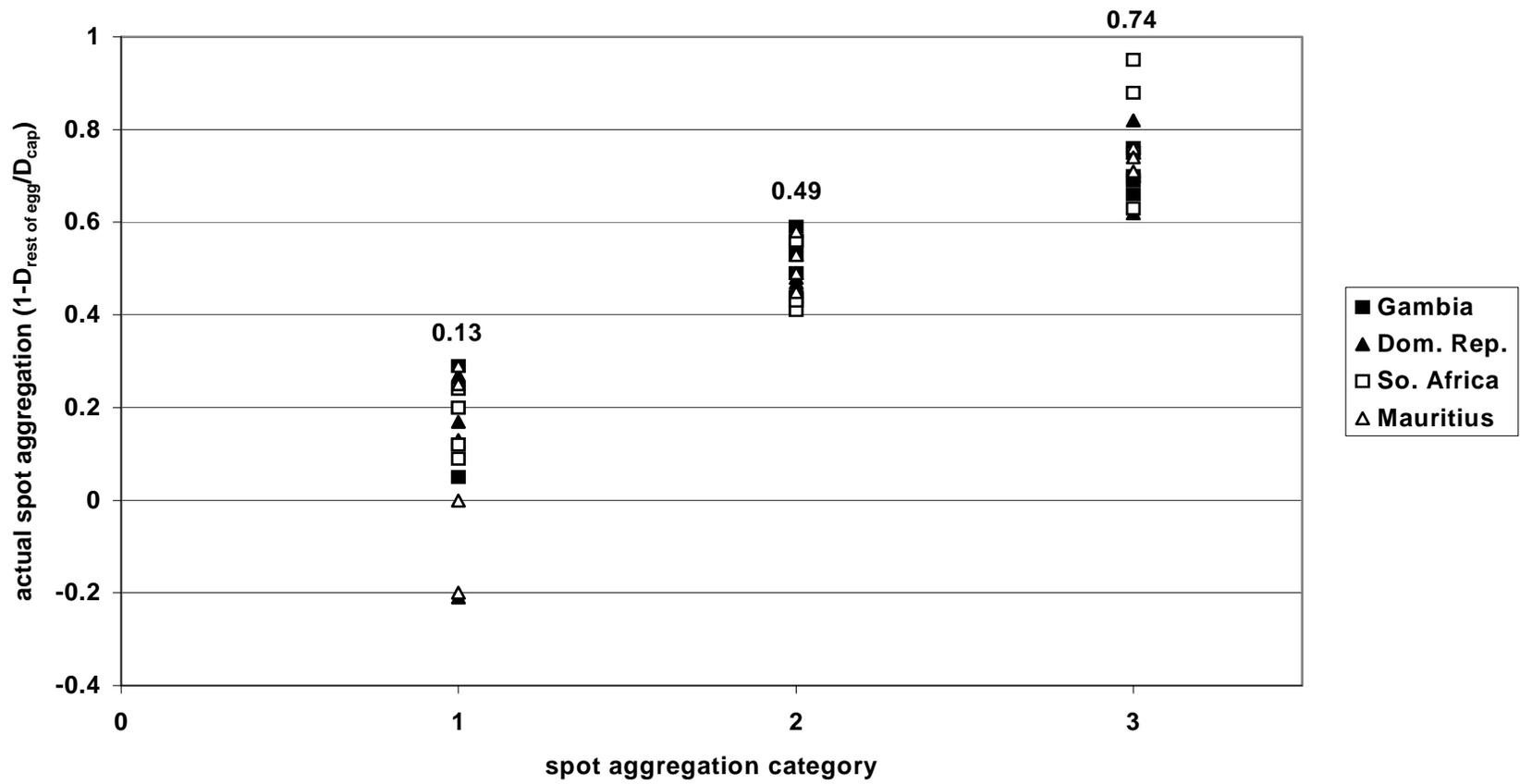


**Fig.6.6. Spot Density in Village Weaver Eggs: Relation of Quantitative Measurements to Index Categories (means above each column)**

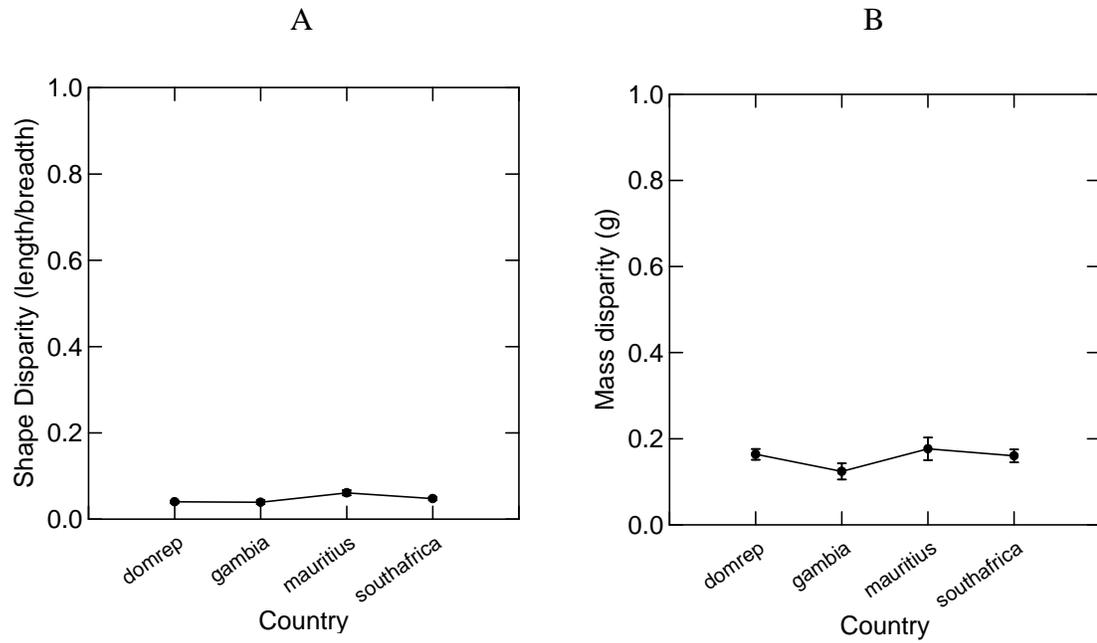


Note: These curves are the mean spectra for each index value. All spots were reddish-brown, and all measurements were taken on blue-green eggs for the sake of uniformity. Lighter spots permit the blue-green to show through the spot, hence the hump peaking near 500 nm.

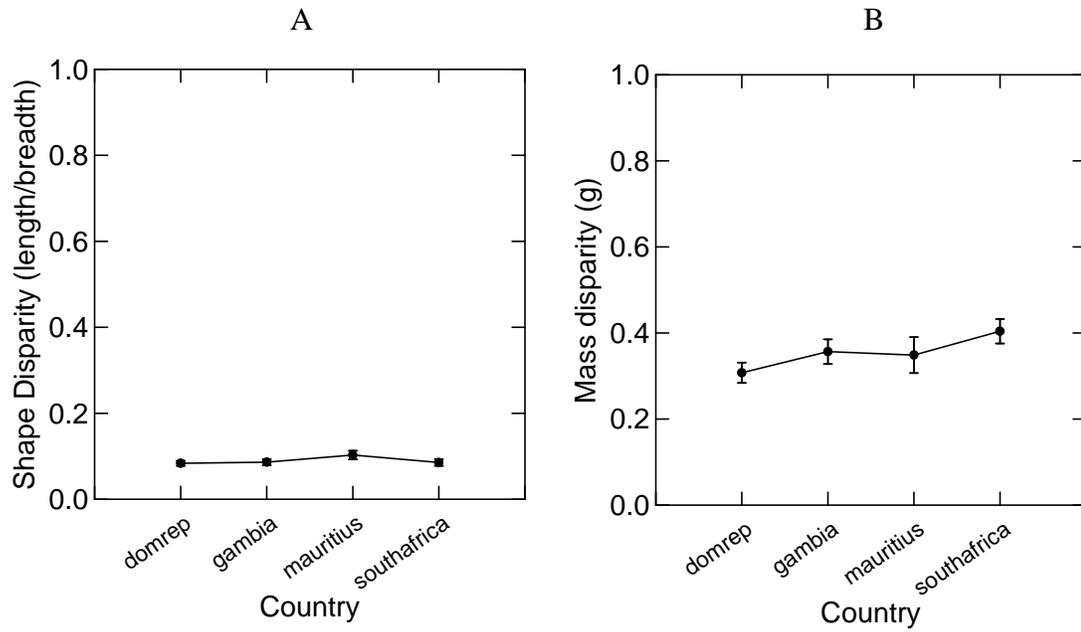
**Fig.6.7. Spot Color in Village Weaver Eggs: Relation of Quantitative Measurements to Index Categories**



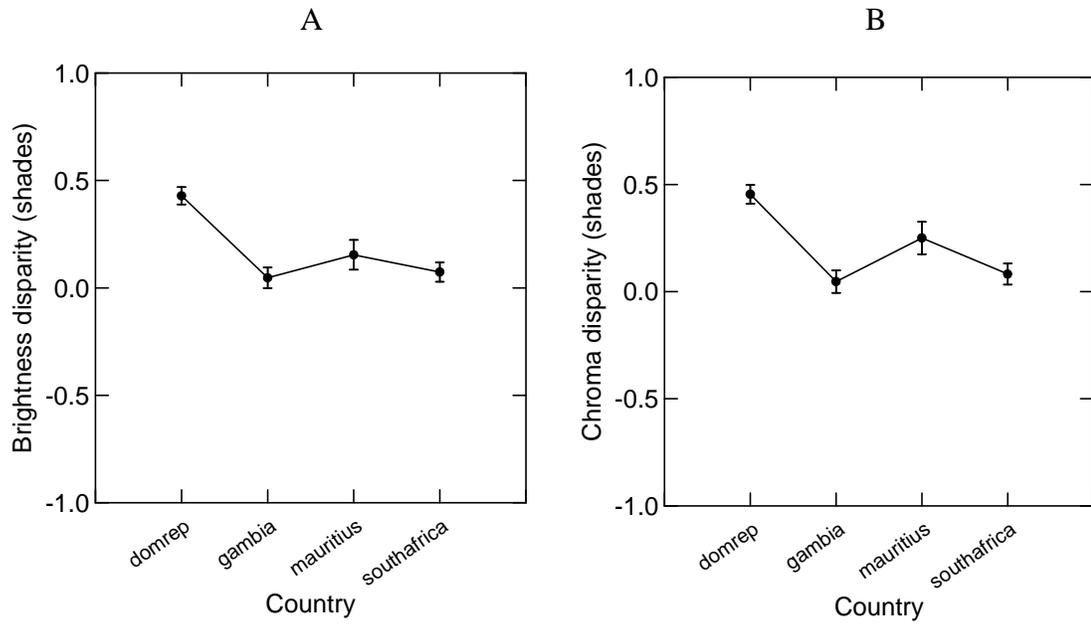
**Fig.6.8. Spot Aggregation in Village Weaver Eggs: Relation of Quantitative Measurements to Index Categories (means above each column)**



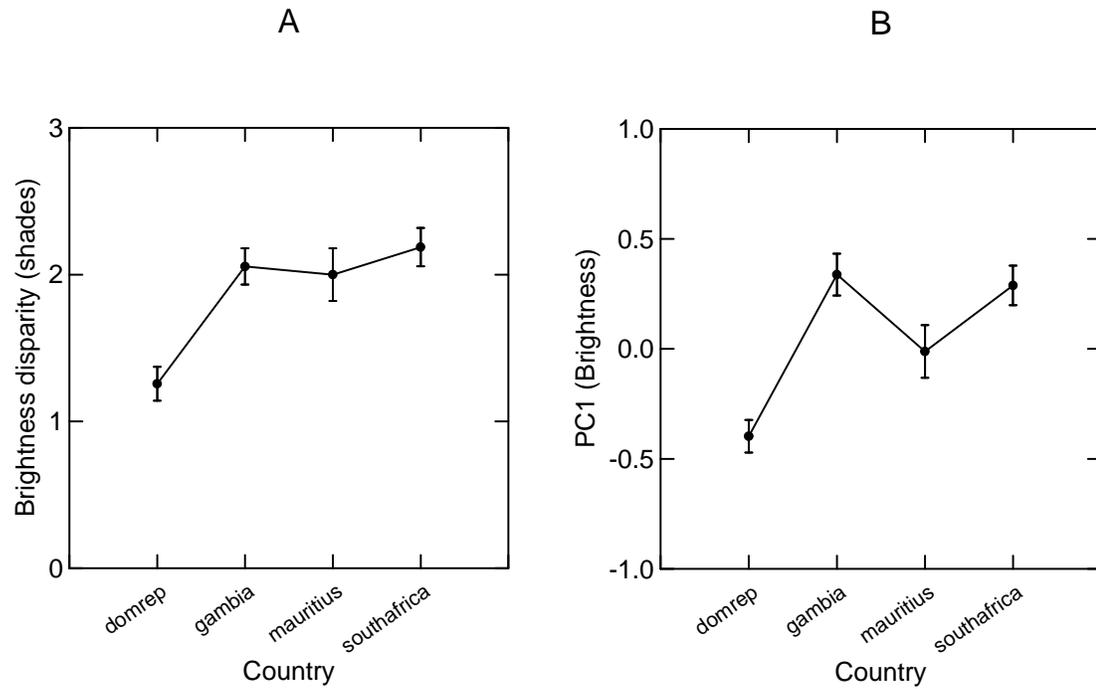
**Fig.6.9. ANOVAs of Within-Clutch Disparity in (A) Egg Shape and (B) Egg Mass Between Village Weaver Populations**



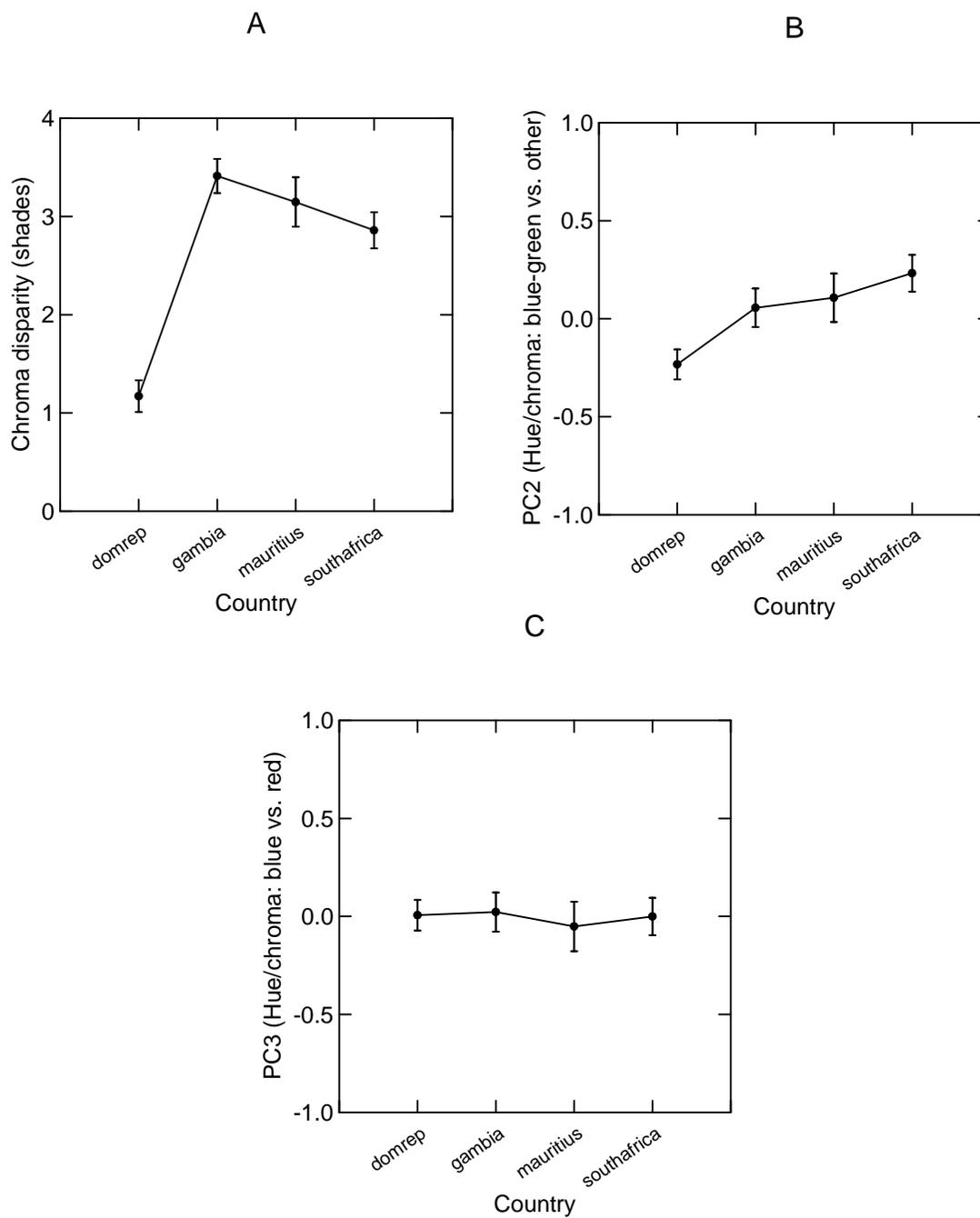
**Fig.6.10. ANOVAs of Between-Individual Disparity in (A) Egg Shape and (B) Egg Mass Between Village Weaver Populations**



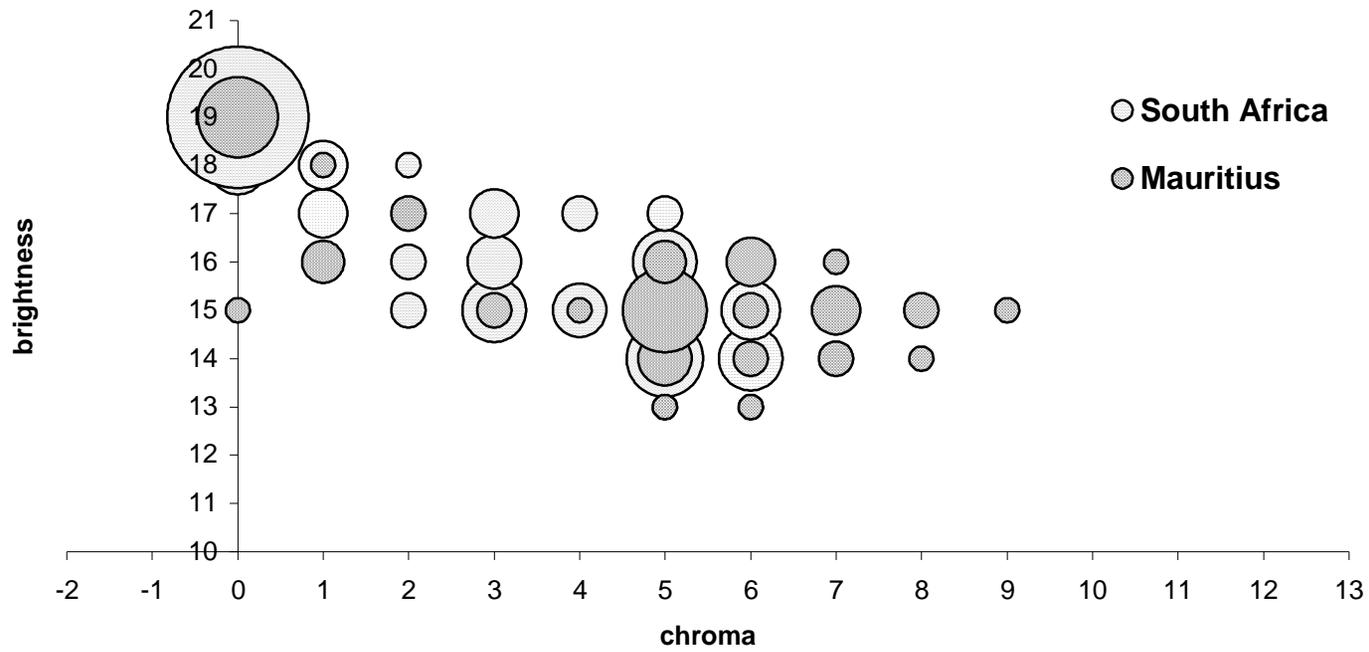
**Fig.6.11. ANOVAs of Within-Clutch Disparity in (A) Egg Brightness and (B) Egg Chroma Between Village Weaver Populations**



**Fig.6.12. ANOVAs of Between-Individual Disparity in Egg Brightness Between Village Weaver Populations, by (A) Color Charts, and (B) Spectrophotometry**

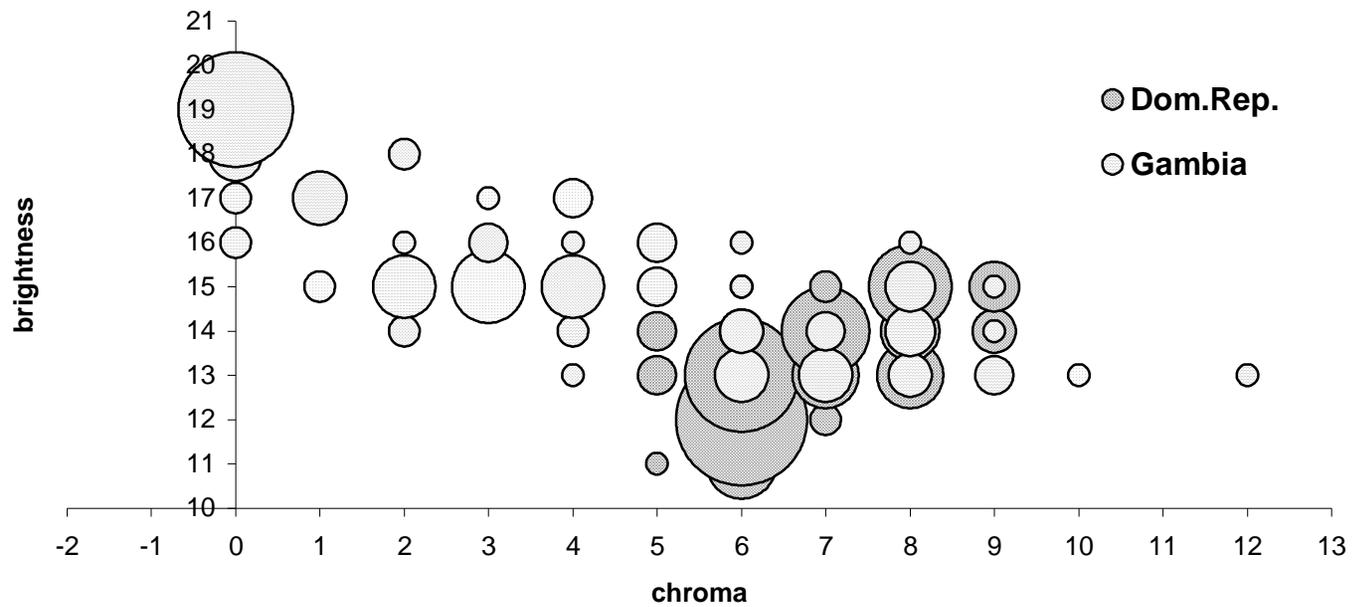


**Fig.6.13. ANOVAs of Between-Individual Disparity in Eggshell Chroma Between Village Weaver Populations, by (A) Color Charts, and (B, C) Spectrophotometry**



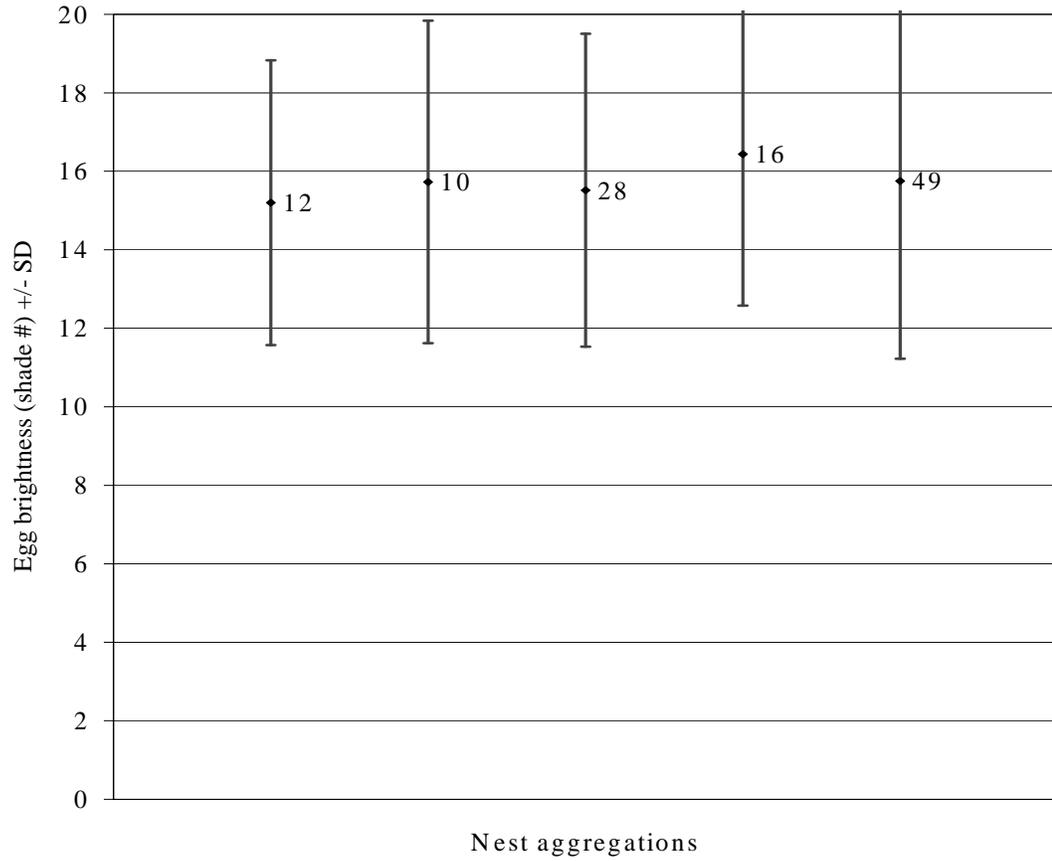
Data assessed with color charts (Villalobos 1947). Bubble sizes represent sample sizes: range 1-34.

**Fig.6.14. Population-Level Egg Color Variability in Village Weavers:  
South Africa vs. Mauritius**



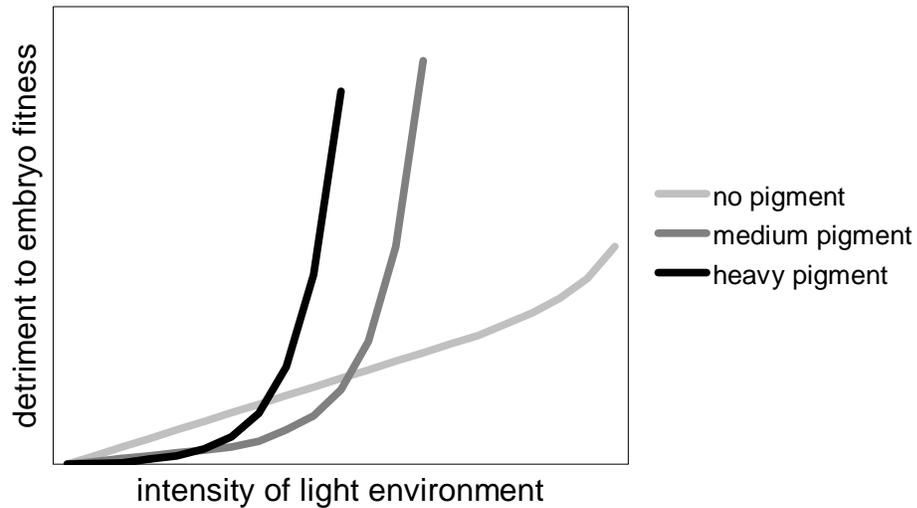
Data assessed with color charts (Villalobos 1947). Bubble sizes represent sample sizes: range 1-35.

**Fig.6.15. Population-Level Egg Color Variability in Village Weavers:  
The Gambia vs. Dominican Republic**



Each point is the mean brightness of the eggs in an aggregation (colony) of weaver nests. Next to each mean is the number of nests in the aggregation. One egg from every nest with eggs was assessed for each aggregation. Brightness shades are from color charts (Villalobos 1947).

**Fig.6.16. Variation in Egg Color Within and Between Village Weaver Nest Aggregations in The Gambia**



According to this model, damage to the embryo can occur through transmitted light or conduction of heat from the shell surface. At low light levels the detriment to fitness correlates with light transmittance through the shell (initial linear portion of each curve). Here the high absorbance of pigment may reduce transmittance to a greater degree than a white egg despite the latter's high reflectance. Absorbance dictates a threshold light intensity for any egg color. Above this threshold the rate of heat accumulation in the shell exceeds the rate of heat loss through convection, and detriment to embryo fitness increases exponentially. The low absorbance of unpigmented eggs results in their being optimal in high-intensity lighting conditions, whereas the high absorbance of pigmented eggs may render them optimal when light is at a lower intensity.

**Fig.6.17. Hypothesized Impact on Embryo Fitness of Different Colors of Eggs in Different Light Environments**

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## CHAPTER 7

### DOES EGG RECOGNITION DECAY IN THE ABSENCE OF CUCKOO BROOD PARASITISM?

Behavior is the product of a particular constitution of an organism's central nervous (or neuroendocrine) system (CNS). For instance, Alcock (1993:116) states: "Genes influence behavior indirectly by affecting the development of the nervous system that individuals have." This does not necessarily mean, however, that the evolution of behavior implies that something in the CNS evolves that has particular relevance to the behavior. Behavior may change as a necessary byproduct of the evolution of some other trait, with no CNS change relevant to the behavior per se. For instance, bill size constrains song production (particularly frequency bandwidth and trill rate) in emberizid finches (Podos 1997; 2001). This constraint means that an evolution of bill size (e.g., Boag & Grant 1981) could lead to a change in song characteristics without any evolution of the central or even peripheral nervous system. The change in song in finches is properly viewed as an *evolutionary* change because the behaviors are part of a "complex co-expressed character set, produced by... genetic change" (West-Eberhard 1989; see also Alexander 1990). In this case bill size can be considered a *modulator* of song characteristics, meaning that bill size has a phenotypic influence on the expression of song characteristics.

In general, any evolution of a modulator of a plastic trait might result in evolution of the plastic trait solely as a byproduct. This includes cases where a behavioral trait is environmentally sensitive, or facultative, in expression, and a modulator of the expression of the trait is part of the individual's own phenotype. If the modulator evolves, the expression of the behavior may change as a direct result. One example is facultative parasitic behavior in bees, which correlates with asynchrony of emergence (van der Blom & Velthuis 1988; Wcislo 1989). If the population were to evolve away from synchrony, parasitism would increase in the population as a consequence. We may assume that the neuroendocrine and physiological pathway leading to the trait's execution does not evolve. In this case, the range of *potential* behaviors given a range of environments would not even have changed. All that would have changed is the distribution of the *expressed* forms of the trait in the population due to the evolution of the modulator, synchrony of emergence. The change in expression is correlated with a genetic change, and thus, perhaps counterintuitively, is evolutionary.

Egg rejection in birds subject to brood parasitism is an example of a trait in which evolutionary change is generally presumed to reflect CNS change, but in fact may simply be a byproduct of the evolution of another trait that modulates its expression; the assumption has never been tested. Rejection of foreign eggs is the behavioral manifestation of a suite of traits including (at least) signature information provided by egg appearance (a morphological trait in the extended phenotype of the mother: see Chapter 6), and a recognition mechanism (a function of the CNS: see Chapter 5). Change in either one of these kinds of traits will result in a change in egg rejection behavior (see below, and Figure 7.1). Several studies have reported change in egg rejection behavior

across generations within a species. Of those, a few either gathered longitudinal data or tested a putative control population to provide a baseline level of egg rejection with which to compare the focal population (e.g. Davies & Brooke 1989a; Briskie et al. 1992; Brooke et al. 1998; Lindholm & Thomas 2000). Whether these changes reflect evolution or plasticity is unknown (Brooke et al. 1998; Payne 1997; Lindholm & Thomas 2000; Rothstein 2001). Although studies that conclude change in rejection behavior usually discuss this in terms of a change in recognition ability, no study has attempted to distinguish this cause from change in egg variability. This might be especially important in species whose brood parasite mimics host eggs (Davies & Brooke 1989b; Payne 1997).

The village weaver *Ploceus cucullatus* is subject to brood parasitism by the egg-mimicking diederik cuckoo *Chrysococcyx caprius* in Africa, lays distinctive eggs in its natural range, and uses the signature information in egg appearance to reject foreign eggs (Payne 1967; Victoria 1972; Collias 1984; Lahti & Lahti 2002). The reliability of this signature information has decayed in two introduced populations in the absence of the diederik cuckoo (Chapter 6). This evolutionary change in egg morphology would necessarily lead to less efficient egg rejection behavior if sympatry were to be reestablished with the diederik cuckoo (Fig.7.1). This is easily explained from the perspective of the cuckoo. A cuckoo has a certain probability of matching the eggs of a host in appearance well enough for acceptance and incubation. This probability is a function of (at least) three things on a proximate level, assuming the cuckoo lays successfully, and randomly with respect to host traits. Egg matching success is (1) negatively correlated with the egg variability in the host population; (2) positively correlated with the egg variability within an individual host; and (3) negatively correlated

with the precision of the egg recognition system in the host. I have shown that the two egg variability traits have changed in introduced populations in allopatry with brood parasitic cuckoos, in the direction that would increase the probability of successful cuckoo egg matching, regardless of whether precision in the recognition system has decayed (Chapter 6). What remains is to determine whether changes in egg rejection behavior between the source and introduced populations can be completely explained as a byproduct of evolutionary changes in egg appearance, or whether additional change in egg rejection behavior occurred. Any change in egg rejection behavior in the introduced populations beyond that which is explained by the evolution of egg appearance, might be attributable either to evolution of the visual-cognitive egg recognition system, or to a further, yet unidentified modulator, such as perception of cuckoos by the weavers (Davies & Brooke 1988; Moksnes & Røskaft 1989).

In this study I compare the rejection behavior of the village weaver in South Africa, in sympatry with the diederik cuckoo, with rejection behavior on Mauritius, an island without egg-mimicking brood parasites where the village weaver was introduced in 1886 and is now abundant (Chapter 4). I also compare rejection behavior in The Gambia, in sympatry with the diederik cuckoo, with that in Dominican Republic on Hispaniola, where the village weaver was introduced more than two centuries ago and is now abundant (Chapter 4), and where there are also no egg-mimicking brood parasites. Since within-clutch variability in egg appearance has increased and between-individual variability has decreased in both populations, extensively so in the Dominican Republic, these changes were controlled (see Methods) in an attempt to separate the portion of behavioral change that might be attributable to perceptual or cognitive changes.

Two studies have previously tested the response of village weavers to the introduction of foreign eggs in one of the populations in this study. Cruz & Wiley (1989) considered the level of egg rejection behavior they observed among Dominican weavers between 1974 and 1982 to be lower than the presumed African level based on indications in Victoria (1972). Cruz & Wiley (1989) therefore classified the village weaver on Hispaniola as an "accepter species". Robert & Sorci (1999) performed egg rejection tests on weavers in the Dominican Republic in 1998, and reported that the level of egg rejection was high, similar to the captive population from Africa studied by Victoria (1972). Robert & Sorci (1999) interpreted the difference between their results and those of Cruz & Wiley (1989) as indicating a rapid increase in rejection behavior by evolutionary and perhaps learned changes in 16 years, due to recent sympatry with the brood parasitic (but not egg-mimetic) shiny cowbird *Molothrus bonariensis*. Others have offered alternative explanations for the results of Cruz & Wiley (1989) (Brooke et al. 1998; Payne 1997; 1998; Rothstein 2001), and the methods used in the two studies differ from each other (see Methods) and from Victoria (1972). The time-sensitive nature of tests of rapid evolution in natural systems makes a true replication impossible. Nevertheless, I will approximate the methods of Cruz & Wiley (1989) and Robert & Sorci (1999) to test the extent to which their results indicate changes in rejection behavior (Rothstein & Robinson 1998; Underwood & Sealy 2002), as opposed to particulars of methodology (Payne 1997; Rothstein 2001).

A cost of rejection is involved if hosts eject their own eggs in the process of removing foreign eggs (Stokke et al. 2002). I report the incidence of costs of rejection in village weavers. I also provide estimates of nest survival.

## METHODS

### *Experimental Parasitism*

I replaced village weaver eggs with conspecific eggs as described in Chapter 5 under "Methods: Experimental Parasitism". The results in Chapter 5 are included in this analysis; those data were gathered on Janjangbureh Island, The Gambia, West Africa (13°35'N, 14°40-50'W; VII-VIII 1999; N=96). Experiments were also conducted near Pietermaritzburg, KwaZulu-Natal, South Africa (29°25-45'S, 30°25-35'E; X-XII 2000; N=102); Black River and Rivière du Rempart Divisions, Mauritius (20°00-20'S, 57°20-40'E; XII 2000 - II 2001; N=59); and Monte Cristi and Valverde Provinces, Dominican Republic (19°35-45'N, 71°00-20'W; IV-VI 2001; N=137) (Fig.6.1). Lack of some measurements (particularly spectra) of some eggs decreased sample sizes for some analyses.

Additional nests served as controls for researcher manipulation and background sources of nest destruction (The Gambia: N=20; South Africa: N=15; Dominican Republic: N=16). All eggs in each of these nests were removed, marked, and replaced in the same nest.

We checked each nest 48-52 h after replacement, with the exception of 54 Gambian nests which were checked 24-28 h after 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 (see Chapter 5). Eggs damaged or missing were considered rejected. All eggs were removed from each nest and measured at the end of the experimental period. All nests were experimentally parasitized during or within 3 days after the female's laying period. Deserted or predated nests were excluded from analysis. Each nest was used only once.

*Egg Measurements*

I took egg measurements as described in Chapter 6 under "Methods: Measurements", including egg shape and mass, eggshell ground color by spectrophotometry and color charts ((VCL: Villalobos-Dominguez & Villalobos 1947), and four eggshell spotting variables. 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 check for associations with egg rejection.

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 (Cuthill et al. 1999). One PCA was performed on the data from all four populations to facilitate interpopulation comparison. Pooling the data into the PCA did not affect results at finer scales: tests within a population or between two populations yielded the same array of significant variables if the PCA was drawn only from those populations. PCA reduced the variation in the data into four orthogonal principal components which were easily interpreted. PC1 explained 61.5% of the variance in the sample. It loaded consistently across the entire (300-700 nm) range of wavelengths, and therefore corresponds closely to differences in brightness, consistent with 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 335-400 nm in wavelength, and PC4 more significantly between 300-335 nm. PC3 explained 3.8% of the variance and represents chroma and hue, mainly contrasting blue-green with longer wavelength colors (see

Appendix for eigenvectors).

Difference between host and experimental eggs in each spotting variable (color, size, density, and aggregation) was calculated as the difference between the categorical values (range 0-3) of that variable that were estimated for the two eggs in the field (all by ARL). Differences of 0, 1-2, and 3 in these variables were partitioned as three levels of a categorical variable. An estimate of how a variable state relates to quantitative difference in spotting (e.g., spots/mm<sup>2</sup> for spot density) was derived from the indexing method described in Chapter 6 (see "Methods: Measurements", and Fig.6.6).

#### *Control for Egg Variability Differences Among Populations*

I employed three means to correct for the increase in within-clutch variation and decrease in between-individual variation in the introduced ranges. (1) In the Dominican Republic, available egg colors did not vary enough for conspecific egg replacements to present the range of cues to hosts (in terms of difference in appearance between host and foreign eggs) that were presented to the source population in The Gambia. The dynamics of rejection of conspecific eggs in Dominican Republic would be at least partially a byproduct of the decrease in distinctiveness of eggs in that population. Moreover, extrapolation from rejection based on existing variation in the Dominican Republic may not provide an accurate representation of potential egg recognition dynamics. Therefore, 71 of the experimental eggs used in the Dominican Republic were painted to match the finish of weaver eggshells, four different colors: one common among Dominican eggs to serve as a control ("dark blue-green", E13/8 in *Villalobos Color Atlas* (VCL: Villalobos-Dominguez & Villalobos 1947); N=17; see Fig.7.2A), one rare among Dominican eggs

but common in Africa ("light blue-green", *VCL*:E15/9), and two other colors common in Africa but absent from the Dominican Republic ("very light blue-green", *VCL*:E17/3; and "off white", *VCL*:19/0; see Fig.7.2B). 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. (2) In both introduced populations, unusual egg appearance variants were especially sought out and used in experiments in order to represent the range of eggs present in the source populations. Results are presented in terms of rejection as a function of differences in color and spotting, so a nonrandom collection of experimental eggs does not introduce bias, as it would if results were presented as an absolute "rejection rate". Introducing a nonrandom collection of eggs does, however, permit analysis of rejection over approximately the African range of egg appearance differences in the introduced populations without a need to extrapolate. Finally, (3) 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 variable. Were the mean egg in the clutch used, some unknown proportion of the decrease in rejection behavior in introduced populations may have been a byproduct of the increase in egg appearance variance within a clutch.

### *Statistical Analysis*

I used logistic regression (LR) (Hosmer & Lemeshow 1989), with SYSTAT<sup>®</sup>10.0 software to relate predictor variables to the incidence of egg rejection and to compare rejection behavior across populations. The fits of the models were assessed by two methods: by McFadden's Rho-Squared ( $\rho^2$ ), and with measures of Sensitivity (*Sns*) and Specificity (*Spc*) provided by SYSTAT 10.0. The  $\rho^2$  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 very satisfactory (Hensher & Johnson 1981). *Sns* and *Spc* capture the overall utility of the model at prediction. *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. Differences among populations in rejection behavior were tested by looking for significant population by trait interactions in a model predicting egg rejection. Hypotheses were tested at the  $P < 0.05$  level of significance.

### *Comparisons Between Studies*

I reanalyzed portions of the Dominican Republic data in an attempt to replicate the methods of prior studies of Dominican village weaver rejection behavior (Cruz & Wiley 1989; Robert & Sorci 1999). Like Cruz & Wiley (1989), I compared rejection rates of hosts whose eggs were different vs. the same as the foreign eggs in the presence or absence of spots. Since Cruz & 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 of the population range. Like Robert & Sorci (1999), I divided egg comparisons into two categories, "mimetic" and "nonmimetic", on the basis of difference in color and spotting. Following Robert & Sorci (1999), these categories were distinguished by visual inspection of the eggs. A second party (ARL) performed all such determinations in the field before the experiments began. Data were excluded if color or spotting differed but not both. Eggs painted colors not found in the Dominican Republic were excluded from both analyses.

This replication is imperfect for at least three reasons. (1) Artificial eggs were used in prior studies but not in the present one. (2) Robert & Sorci (1999) introduced two foreign eggs to a nest (one an artificial cowbird egg) whereas Cruz & Wiley (1989) and I only introduced one. The prior studies report that these two factors did not influence their results. Finally, (3) the earlier studies described egg color subjectively, so their relation to the spectral data presented here is uncertain.

## **RESULTS**

### *Background Nest Destruction*

Of 445 nests monitored for two days, 29 (6.5%) were destroyed or predated (Gambia: 9 of 116 (7.8%); South Africa: 10 of 117 (8.5%); Mauritius: 7 of 59 (12%); and Dominican Republic: 3 of 153 (2%)). Of 51 control nests, 4 (7.8%) were among those destroyed. A hailstorm of highly unusual severity (according to local farmers) destroyed four nests in South Africa and killed the incubating female at a fifth. I alternatively excluded and included these five cases with the other cases of nest loss to provide a

range. Assuming that our activities did not influence the probability of nest failure, and also that each two day period is equal in nest survival (0.935-0.945), an estimated 62-67% of village weaver nests averaged over all four populations would survive the 14 days (Collias & Collias 1970) of laying and incubation. Given a 20 day nestling period (Collias & Collias 1970), if the rate of destruction is consistent, 32-38% of nests initiated would survive to fledging. Causes of egg or nestling mortality besides nest destruction and predation are not considered in this estimate. This survival estimate would be biased downward if some locations are consistently safer than others, such that nests tend to fail disproportionately early in the nesting cycle; but it would be biased upward if parental feeding or nestling begging calls attract predators. Nevertheless, considering the potentiality of further losses due to egg failure and starvation, this estimate is roughly consistent with that of Collias & Collias (1971) that 25-30% of nests fledge young on average.

### *Egg Rejection Controls*

Of 45 surviving control nests, clutches were intact in 43 at the end of the experimental period, suggesting that our manipulation did not have a strong effect on the integrity of a clutch or the rejection behavior of the host. Of 16 surviving nests tested with painted eggs intended to mimic host eggs in the Dominican Republic, the egg was accepted in 15, indicating that paint was an adequate substitute for natural coloration for egg recognition purposes, and that a lack of mimicry in UV reflectance 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.

### *Rejection Costs*

A host egg was rejected with a foreign egg in 12% (22 of 185) of the rejections (Gambia: 13 of 52 (25%); South Africa: 5 of 45 (11%); Mauritius: 1 of 31 (3%); and Dominican Republic: 3 of 57 (5%)). In only one case (in the Dominican Republic) did a bird reject her own egg but leave a foreign egg in the nest.

### *Predictors of Egg Rejection*

Four variables were significant predictors of rejection in the combined analysis of all four village weaver populations: the difference between foreign and host eggs in brightness, visible hue/chroma, and spot density; and whether or not an egg was laid during the experimental period (LR:  $N=348$ ,  $P<0.00001$ ,  $\rho^2=0.216$ ,  $Sns=0.61$ ,  $Spc=0.66$ ; Table 7.1). On the basis of the odds ratios associated with logistic regression analysis, a village weaver was on average 88% more likely to reject a foreign egg for each unit it differed from its own eggs in brightness as judged by the PC1 values, which ranged from -1 to 4. The value of 1.81 (95% C.I.: -0.08, 4.31) was the LD50, or the value at which an experimental egg would be rejected with 50% probability if all other egg appearance aspects did not differ. A village weaver was also on average 56% more likely to reject a foreign egg for each unit of difference in hue/chroma as judged by PC3, which ranged from -4 to 3. The LD50 was 0.00 (95% C.I.: -2.05, 2.35). For examples of how PC1 and

PC3 values translate into spectral differences, see Fig.7.3. For graphical representations of egg rejection by differences in color see Figs.7.4, 7.5.

These measures of brightness and hue/chroma are not directly comparable to those drawn from color charts, since principal components are orthogonal to each other, whereas brightness and chroma as judged by the *Villalobos Color Atlas* are intercorrelated (Pearson correlation = 0.71). Nevertheless, I substituted color chart brightness for PC1 and color chart chroma for PC3 for two populations (The Gambia and Dominican Republic). The two models were similar, although the one based on color charts was slightly superior (LR: PCA:  $N=206$ ,  $P<0.00001$ ,  $\rho^2=0.234$ ,  $Sns=0.59$ ,  $Spc=0.70$ ; color charts:  $N=206$ ,  $P<0.00001$ ,  $\rho^2=0.281$ ,  $Sns=0.62$ ,  $Spc=0.72$ ). The odds ratio for PC1 (2.46) was 80% higher than that for color chart brightness (1.36), indicating that one shade of difference in color is approximately equivalent to 1.8 units in PC3 in terms of the likelihood of egg rejection. The odds ratios were similar for PC3 vs. color chart chroma (1.35), indicating that one color chart shade is roughly equivalent to one principal component unit in predicting egg rejection.

Birds were on average 9.1 times more likely to reject an egg if it differed from their own eggs by a mean of 4.2 spots/mm<sup>2</sup> (estimated from our index values: see Fig.6.6) rather than being the same in spot density (mean difference 0.05 spots/mm<sup>2</sup>). They were 3.3 times more likely to reject an egg if it differed by a mean of 0.6 spots/mm<sup>2</sup> relative to when it was the same (Fig.7.6). Rejection of eggs that differed by an average of 0.6 spots/mm<sup>2</sup> would be predicted with 0.13 probability, and 4.2 spots/mm<sup>2</sup> with 0.30 probability, if all other egg appearance features were identical. All spotting variables were found to be correlated (Spearman correlation 0.69-0.76,  $N=353$ ), so although other

spotting variables were not significant when spot density was in the model, spot density is not necessarily the only spot characteristic used by village weavers for rejection.

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, of 273 nests where laying was completed before the experiment began, 139 (51%) of experimental eggs were rejected; whereas of 81 nests where at least one egg was laid during the experimental period, only 26 (32%) of experimental eggs were rejected.

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, were also not significant in the combined model.

#### *Population Differences in Egg Rejection*

In the combined four-population model presented in Table 7.1, interactions with population were not significant. Nevertheless, adding the interaction between population and difference in brightness to that model indicates a slight but significant difference in the use of brightness among populations (LR:  $N=348$ ,  $P<0.00001$ ,  $\rho^2=0.238$ ,  $Sns=0.62$ ,  $Spc=0.67$ ; Mauritius vs. South Africa  $P=0.044$ ; Dominican Republic vs. South Africa  $P=0.048$ ). 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, 6 df,  $P=0.10$ ;  $\rho^2$  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 the difference

between South Africa and other countries (South Africa vs. Mauritius:  $P=0.03$ ; vs. Dominican Republic:  $P=0.03$ ; vs. The Gambia:  $P=0.14$ . All other pairs:  $P>0.25$ ). The coefficients are positive and the odds ratios greater than one for all of the comparisons with South Africa (South Africa being the reference in dummy coding), indicating that the effect of brightness on rejection was lower in South Africa than in the other populations. No interactions between population and any other variable were significant in two-population models.

Single-population models permit comparison among populations in the kinds of variables that are significant at predicting egg rejection (Table 7.2). The significant variables in all models were a subset of the variables of the combined model (Table 7.1) except for spot size in the Dominican Republic, which is correlated with spot density and near significance in the combined model. Each model  $P$  value, average of  $Sns$  and  $Spc$ ,  $\rho^2$ , and the significance level of the strongest predictors are in rank order of sample size across the four populations, without exception. The absence in single-population models of some variables significant in the full model might therefore be explained by differences in statistical power across populations. PC1 (brightness) was not significant for South Africa alone, consistent with the effect found in the two-population and four-population models.

### *Comparisons Between Studies*

Combined results from artificial and natural village weaver eggs in the Dominican Republic from Cruz & Wiley (1989) indicate 11.7% rejection (7 of 60) 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% (8 of 52) eggs were rejected. All eggs differed randomly in color as well, up to half of the population range. With similar criteria applied to the data in the present study, the percentages of eggs rejected were 6.6% (4 of 61) and 15.0% (2 of 17), respectively (Table 7.3).

Artificial eggs placed into Dominican weaver nests by Robert & Sorci (1999) were rejected 16.0% of the time (4 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% (3 of 34) and 64.3% (18 of 28) (Table 7.4).

## DISCUSSION

### *Factors Influencing Egg Rejection*

Color and spotting variables, but not egg size, egg shape, or microhabitat variables, were significant factors influencing village weaver rejection of foreign eggs, as previously found in The Gambian population alone (Lahti & Lahti 2002; see also Victoria 1972), and as predicted from the differential reliability of egg features as signature information (see Chapter 6). Spectral analysis permitted the division of color into various components. The component with the greatest influence on egg rejection was brightness (average reflectance across all light wavelengths), although the birds also used hue or chromatic variation.

As indicated by the use of painted eggs that mimicked natural eggs in the human-visible range, lack of UV reflectance in foreign eggs was not sufficient by itself to elicit

egg rejection. A larger-scale study on this point would be required to determine whether presence or absence of UV reflectance was a factor at all. However, the proportion of UV variation that was orthogonal to variation in longer wavelengths did not influence rejection, as two principal components of the spectral data from the entire dataset represent such variation. Although this may seem at variance with recent studies that have shown the importance of UV reflectance to bird behavior (e.g. Bennett et al. 1997; Hunt et al. 1999; Church et al. 1998), in fact those studies and this one tested for two different things. Those studies compared normal behavior to that when UV reflectance was experimentally blocked. Such a method is a test for the importance of *any* reflectance in the UV. The nonsignificance of the UV-related principal components in spectral analysis in this study, on the other hand, indicates that the proportion of UV reflectance differences that were orthogonal to, or nonredundant with, reflectance differences in the human-visible portion of the spectrum were not important in predicting egg rejection. Significant variation among egg colors existed in the 300-400 nm range that was independent of differences in the remainder of the bird visible range, but this variation was not important to egg rejection. Studies that block UV show that some UV reflectance is important, but do not show that the information in that range is nonredundant with information in the remainder of the spectrum. Blocking UV may in fact be creating nonredundant information in the UV portion of the spectrum (lack of reflectance can itself be information), which may influence bird behavior more than UV wavelengths would under natural conditions.

I did not detect the use of brightness in the rejection of eggs in South Africa, despite it being the strongest color-related predictor in all three other study areas.

Hue/chroma, on the other hand, was a more powerful predictor, in the human-visible wavelengths and to a lesser extent in the near-UV. This phenomenon may be explained by the fact that experiments in South Africa were initiated under cloud cover and during rain much more frequently (70 of 115 nests: 61%) than in the other study areas, where nests were usually in full sun all day (weather was cloudy during initiation of experiments in Mauritius at 0 of 56 nests; Dominican Republic: 10 of 149 (7%); The Gambia: 13 of 57 (23%)). Moreover, unlike in the South African study site, cloud cover and rain in The Gambia were ephemeral, such that the nests were in full sun for the majority of every study day. South African nests, therefore, were regularly in a condition of low light, which is deficient in brightness. Differences in chroma and hue of eggs, moreover, might be more conspicuous in an overcast day since the ambient light in the nest would be whitish (i.e., roughly equally reflective at all wavelengths) rather than having the more chromatic irradiance characteristic of filtered sunlight (Endler 1993; Endler, personal communication). The difference in the portion of the signature information used to reject eggs in South Africa relative to the other study sites may therefore reflect differences in perceptual ability in different light environments.

The finding that eggs are more likely to be accepted if introduced to the nest during the laying period could indicate that some weavers wait longer to reject eggs when parasitized at that stage. Alternatively, weavers might be less likely to reject eggs at all when they are parasitized during the laying stage (Welbergen et al. 2001). I did not follow most nests beyond the 48-52 h experimental period, and so cannot distinguish between these two alternatives. No interactions with egg appearance differences were significant, which rules out the possibility that birds with incomplete clutches that were

parasitized with more similar eggs delayed in rejecting them until more eggs were laid. Since diderik cuckoos commonly parasitize hosts during the laying stage (Skead, 1995; Lawes & Kirkman 1996), a failure of some birds to reject foreign eggs laid during their laying stage would be maladaptive. Perhaps the circumstance of viewing one's complete clutch may aid in egg recognition, especially in younger birds if they have poorer egg recognition (Lotem et al. 1995). Weavers do not need their own eggs to be present in the nest at the time of parasitism in order to reject eggs (Lahti & Lahti 2002), but they may nevertheless benefit by having laid and observed them during that nesting attempt. Victoria (1972) observed that village weavers frequently manipulate their eggs from the time they lay their first one. This behavior may familiarize the birds with their eggs and facilitate egg recognition in the event of parasitism.

All significant predictors together produced a highly significant model, but one with a moderate level of predictive power, though better than average for evolutionary studies (Møller & Jennions 2002; e.g., *Sns* and *Spc* values in the 0.60-0.70 range even with other, marginal, variables included). This suggests that other variables, unaccounted for in this study, are also influencing egg rejection behavior. Nevertheless, like Victoria (1972), after hundreds of egg replacements we were able to predict correctly in most cases whether an egg would be rejected or accepted before the experiment was run. It is likely that our methods of assessing color and spotting, though extensive and quantitative, are still unable to approximate well the integration of egg appearance in the mind of the bird. Researchers working on assessment of bird song deal with similar difficulties (Khanna et al. 1997; Payne et al. 2000). Moreover, we did not assess sources of variation

between host individuals (e.g., some individuals might be better discriminators than others), or within an individual (e.g., varying with environment or experience).

*Dynamics of Rejection Behavior upon Removal from Cuckoo Brood Parasitism*

Rejection behavior decays after removal of a weaver population from sympatry with an egg-mimicking brood parasite, both after 115 years, and after at least 200 years (Chapter 6, and Fig.7.1). However, all of this decay is explained by differences in egg variability among the populations, rather than by a decline in the visual or cognitive system responsible for egg recognition. The loss of precision in egg rejection is a behavioral byproduct of the loss of precision in signature information. Given the same degree of difference between host and foreign eggs as would be possible in the source population, and given a restoration of within-clutch uniformity, no decline in rejection behavior would be evident on Mauritius relative to South Africa, or on Hispaniola relative to The Gambia.

This result also suggests that environmental features that differ between the source and introduced populations are not significant modulators of egg rejection in weavers. For instance, the diderik cuckoo was present at study sites in The Gambia and South Africa, but its proximity did not increase rejection behavior relative to that of weaver populations in the absence of the cuckoo. Possible exceptions to the nonsignificance of environmental features include any features associated with actual cuckoo parasitism events, since I did not simulate those features in the source populations. For instance, this study does not adequately test for the effect of a cuckoo in or at a host nest.

Egg recognition ability has therefore remained latent in the Mauritian and Dominican population, despite the fact that it has lost much (at least) of its functionality, in two respects. First, egg appearance evolution in the introduced populations has decreased the reliability of the signature information used in egg recognition. Considering the difference between the loss after 100 years that after >200 years, this decline could still be continuing in these populations. So, some degree of the capacity for egg recognition that still exists in the introduced ranges cannot be utilized because it has been compromised by the decay of other components of the functionally integrated suite of traits.

The second sense in which the persisting trait has lost functionality is that the main function has disappeared: the predominant agent rendering egg recognition adaptive is missing in the introduced populations. Egg appearance variability and egg rejection behavior in this species has been maintained by diderik cuckoo parasitism (Chapter 6), which suggests that the level of egg recognition ability observed in the introduced populations, where the cuckoo is absent, would have lost functionality even if egg appearance evolution had not compromised its efficiency. The only brood parasite on Hispaniola is the shiny cowbird (Post & Wiley 1977), which in the Greater Antilles lays eggs that are white and spotted (Biaggi 1983; Cruz & Wiley 1989). This is far different from the appearance of any weaver eggs on Hispaniola; rejection of shiny cowbird eggs does not require the village weaver's level of egg recognition ability.

Egg recognition could still be functioning in the introduced populations as a defense against conspecific brood parasitism. Although we did not observe conspecific brood parasitism, it may exist, and weavers might reject conspecific eggs in nature.

Nevertheless, any selection imposed on egg recognition by conspecific parasitism would have to be very weak. Conspecific parasitism avoidance would have to be maintaining egg recognition ability but failing to maintain the egg appearance characteristics that give that egg recognition functionality. As egg signature information declines in reliability, any selection on egg recognition necessarily weakens because the adaptiveness of egg recognition is limited by signature information.

### *Replication of Prior Studies*

Replications of the methods of both Cruz & Wiley (1989) and Robert & Sorci (1999) produced results that were qualitatively very similar to those in the original studies, in terms of percent of eggs rejected in different treatments. This suggests that my approximation of their methods was adequate, and that experimental date (1974-2001) has not had an influence on the results of the three studies. More importantly, it indicates that the differences in conspecific egg rejection rates of Dominican weavers between Cruz & Wiley (1989), Robert & Sorci (1999), and the present study, are entirely due to differences in methodology rather than temporal changes in weaver egg rejection behavior.

This finding has several implications. Cruz & Wiley (1989) report a decline in rejection behavior relative to that presumed of the African source population. They were correct in assuming a high level of rejection of conspecific eggs in the African population (Lahti & Lahti 2002). However, their low levels of rejection of conspecific real and model eggs were due to two factors: (1) their choice of how to vary experimental eggs from host eggs, and (2) the evolution of egg appearance in Dominican weavers. Since

the second of these factors necessarily influences the efficiency of egg rejection, Cruz & Wiley (1989) are correct about there having been a decline in egg rejection behavior, though they were incorrect in their characterization of the Dominican village weaver as an "accepter species". Robert & Sorci (1999) report a rapid increase in rejection of conspecific eggs in Dominican weavers over a 16 year period. The fact that a replication of their methods and those of Cruz & Wiley (1989) yield results similar to those of the original studies show that in fact no detectable change in this trait had occurred in the population during that time period. The higher levels of rejection behavior observed in Robert & Sorci (1999) are most likely due to the fact that their choice of how to vary experimental eggs from host eggs captured more (probably all) of the population variability that exists in the Dominican Republic, whereas the methods of Cruz & Wiley (1989) only captured a small subset of this variability.

This analysis prompts at least two suggestions for future studies: (1) in egg rejection experiments, difference between host and experimental eggs should be quantified; and (2) the use of a flat "rejection rate", percentages of eggs rejected vs. accepted (even in conjunction with the terms "mimetic" and "nonmimetic"), does not have relevance for a brood parasite - host system where either the host or the parasite has variable eggs.

#### *Implications for an Understanding of the Evolution of Behavior and Morphology*

Investigations into traits under selection in various organisms have demonstrated correlated evolution of morphological and behavioral traits (Emerson & Koehl 1990; Losos 1990; Bauwens et al. 1995; Jiggins et al. 2001; Hastings 2002). Two issues raised

by such correlations are the nature of the behavioral evolution, and the order of the evolution of the two traits. In fact the important distinction is not between behavior and morphology per se, but between a plastic trait and another trait that modulates or constrains it. Because behavioral traits tend to be prime examples of plastic traits (West-Eberhard 1989; 2003), and are of course constrained by associated morphological features, the behavior-morphology distinction will be used here as a special, but common, case.

The present study demonstrates a case of the evolution of behavior as a byproduct of the evolution of a morphological trait that modulates its expression. Despite its probable ubiquity, this mechanism of correlated evolution may not yet have been given a name: it might simply be called *byproduct evolution*. Its distinctiveness can be illustrated by contrast with another mechanism: *phenotypic accommodation* as described by West-Eberhard (1989; 2003). She describes phenotypic accommodation as a change in a plastic trait correlated with evolution in another trait when the change in the plastic trait involves a "change in developmental pathway" or a "new phenotypic subunit or modular trait". In other words, the response is active, or functional. The change in behavior in the present study was not functional, but was a direct and necessary consequence of a change in certain morphological traits (of eggs), given the current interactions among these traits. The distinctiveness of the behavioral evolution in the present study is thus that the village weaver did *not* accommodate to the change in signature information. In the finch and bee examples provided in the Introduction this would also be the case. In those cases, the current state of trait interactions necessitates that finch trill rate decreases when bill size increases, and bee parasitism increases when synchrony decreases. Behavior would

change in those cases, and such change would correlate with genetic change and would therefore be evolution, though it is distinct from phenotypic accommodation.

In phenotypic accommodation, there is functionality to the plastic change per se; the organism adjusts "in response to" the change in the modulating trait, and a different developmental pathway is initiated. Byproduct evolution, on the other hand, can be characterized by a lack of buffering or compensating action on the part of the organism; change in the focal trait would be solely as predicted by the change in the modulator. Such instances of behavioral change may be trivial in a mechanistic (physiological, developmental) sense, but they cannot be ignored because they are not trivial in an evolutionary sense. Evolution of egg rejection behavior as a byproduct of decline in egg variability, for instance, is evolutionary change since the modulator (egg variability) has evolved; and the change has potential fitness impacts in the context of brood parasitism.

Testing for byproduct evolution in a behavior can be relatively simple at times. For instance, certain *Heliconius* butterfly sister species have diverged in color pattern to mimic two different model species. This evolution has correlated with divergence in mate choice based on color pattern. (Jiggins et al. 2001). The mechanism of behavioral evolution in this case has not been determined, but byproduct evolution cannot account for it; i.e., the divergence in mate choice cannot be predicted solely from a direct phenotypic effect of the change in color pattern. (In a species with post-hatching parental care, on the other hand, passive accommodation might explain such a correlation if females choose males that resemble their fathers.) The next step would be to test whether phenotypic accommodation is operating. Whether an instance of behavioral evolution is solely a byproduct, or involves some change independent of the immediate effect of

associated morphology is seldom tested, but such tests could lead to a deeper understanding of trait evolution and coadaptation.

A second issue highlighted by the correlation of behavior and morphology is the order in which these traits evolve. When the order can be inferred, studies often find support for the contention of Mayr (1960) that behavioral change usually precedes morphological change (Wcislo 1989; Prum 1990; McPeck 1995; West-Eberhard 2003). This is a plausible, but yet untested, hypothesis for the evolution of egg recognition and egg polymorphism in birds as well. However, this study together with Chapter 6 shows that in allopatry with the cuckoo, morphology has been lost but behavior (that portion not a byproduct of the morphology) has been retained. Wiens (2000) likewise found decline of morphology but not behavior in phrynosomatid lizard displays, and considered this to be contrary to predictions based on Mayr (1960) and subsequent supporting work (see Wcislo (1989), and references therein). In Mayr (1960), however, the behavior-precedes-morphology hypothesis was associated with the concept of *novelty*, and still is today (West-Eberhard 2003). Novelty is a difficult concept to define. Nevertheless, there may be reason to predict that the relative sequence of morphological vs. behavioral evolution will depend on whether a trait's functional integrity is increasing or decreasing (when such a distinction can be made). Perhaps when a suite of correlated traits is *losing* functional integrity, i.e. selection is not maintaining it, the morphological traits may decay faster than the behavioral, for the following two reasons.

First, selection may act towards the decay of a nonfunctional trait directly only when the trait is expressed. A trait that is latent is ecologically irrelevant, and so incurs no cost beyond that of maintaining the potentiality for expressing the trait (associated

neural connectivity or circuitry, for example). If behavior tends more than morphology to be conditionally expressed and therefore latent in the absence of functionality, one would predict morphology to decay more rapidly than behavior, in general. If morphology tends to bear a more significant physiological maintenance cost than latent behavior, this too should lead to faster morphological than behavioral decay. In the case of egg recognition vs. egg variability, egg recognition remains unexpressed unless a female rejects her own viable eggs. Whether this occurs in weavers or other species is unknown (Rothstein & Robinson 1998). Egg appearance, in contrast, cannot be "turned off". It is always ecologically and physiologically relevant and therefore potentially subject to direct selection. I have hypothesized sources of selection on egg color and spotting in the introduced weaver populations in Chapter 6.

Second, traits may persist without being maintained by selection if they are correlated with traits that are. If nonfunctional morphological traits are less likely to be phenotypically correlated with functional traits than nonfunctional behavioral traits are, morphological traits will tend to decay at a faster rate. Recognition systems, at least, are thought to be integrated and used for several purposes (Basolo & Endler 1995), so correlation with functional recognition traits may cause egg recognition to persist. Egg color and spotting, on the other hand, is administered by a specialized pigment epithelium that could apparently lose functionality without affecting other functional traits. This greater buffering of behavior rather than morphology to decay may be a general pattern, especially if the morphology in question is a derived specialization, and if the behavior is a function of a cognitive system that could be used for other purposes.

These considerations may explain why some have observed slow or nonexistent decay of egg recognition (Rothstein 1990; 2001) and other behavioral traits (Coss 1999) in the presumed absence of selection pressure. I hypothesize that many morphological features, including egg variability, are more likely to experience direct negative selection, and less likely to be phenotypically correlated with functional traits, than behavioral traits are; if so, morphological traits should decay more rapidly than behavioral traits upon loss of functionality. If this is true, the predominant idea that "behavior takes the lead in evolution", or even that "more plastic traits take the lead in evolution", is inadequate because it incorrectly assumes that evolution is always moving a particular trait towards increasing functional integration and functionality.

<b>Predictors</b>	<b>Estimate</b>	<b>S.E.</b>	<b>Odds Ratio (95% C.I.)</b>	<b>P</b>
(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 Expt.	0.89	0.31	2.44 (1.32-4.52)	0.005

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 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 quantitative interpretation of levels). For "Egg Laid During Expt.", the Odds Ratio is the factor by which rejection is more likely when the host has already completed her clutch relative to when she is still laying during the experiment.

**Table 7.1. Foreign Egg Rejection on the Basis of Egg and Clutch Characteristics:  
Four-Population Combined Logistic Regression Model**

Population	<i>N</i>	<i>P</i>	$\rho^2$	<i>Sns</i>	<i>Spc</i>	Predictors	Estimate	SE	Odds Ratio (95% C.I.)	<i>P</i>
South Africa (source)	94	0.00002	0.190	0.61	0.64	Spot Density (Low)	-2.34	0.58	0.10 (0.03-0.30)	0.00005
						Spot Density (Medium)	-0.71	0.70	0.49 (0.12-1.95)	0.31
						PC3 (Visible Hue/Chroma)	0.38	0.22	1.46 (0.94-2.26)	0.088
						[PC4 (Low Near-UV)] [Spot Size]				
Mauritius (introduced)	52	0.002	0.133	0.64	0.51	PC1 (Brightness)	1.62	0.67	5.08 (1.37-18.9)	0.015
						[PC2 (High Near-UV)]				
The Gambia (source)	72	0.001	0.186	0.55	0.69	PC1 (Brightness)	0.80	0.33	2.22 (1.17-4.22)	0.014
						PC3 (Visible Hue/Chroma)	0.76	0.37	2.13 (1.04-4.40)	0.040
						Spot Density (Low)	-2.53	1.23	0.08 (0.01-0.88)	0.039
						Spot Density (Medium)	-2.27	1.24	0.10 (0.01-1.18)	0.067
						[Egg Laid During Expt.]				
Dominican Republic (introduced)	133	<0.00001	0.292	0.64	0.72	PC1 (Brightness)	1.07	0.22	2.90 (1.87-4.51)	<0.00001
						Spot Size (Low)	-2.23	0.54	0.11 (0.04-0.31)	0.00004
						Spot Size (Medium)	-1.67	0.57	0.19 (0.06-0.58)	0.004
						Egg Laid During Expt.	1.09	0.50	2.98 (1.12-7.95)	0.029

The *P*-value in the third column is the probability that the variables predict egg rejection better than a constant alone.  $\rho^2$  (McFadden's Rho-Squared) estimates explained variance, but returns lower values than the  $R^2$  of linear regression: values between 0.20 and 0.40 are considered desirable (Hensher and Johnson 1981). *Sns* is the probability of the model accurately accepting a true response; *Spc* is the probability of accurately rejecting a false response. Color and spotting predictors refer to difference between host and foreign (experimental) eggs. Predictors in brackets approached significance ( $P < 0.15$ ) but were not included in the model. The Estimate is the value of the coefficient in the LR equation; it is presented with associated Standard Error and *P*-value. For color variables, the Odds Ratio (with its associated 95% Confidence Interval) is the factor by which egg rejection increases for a one unit increase in the predictor variable (PC). For "Spot Size" and "Spot Density", the Odds Ratio is the likelihood of rejection at low or medium spot density differences relative to high difference. For "Egg Laid During Expt.", the Odds Ratio is the factor by which rejection is more likely when the host has already completed her clutch relative to when she is still laying during the experiment.

**Table 7.2. Foreign Egg Rejection on the Basis of Egg and Clutch Characteristics:  
Single-Population Logistic Regression Models**

<b>Data from Cruz &amp; Wiley 1989</b>				
	accepted	rejected	<i>N</i>	% rejection
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
<b>Data from this study</b>				
	accepted	rejected	<i>N</i>	% rejection
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)	15	2	17	15.0

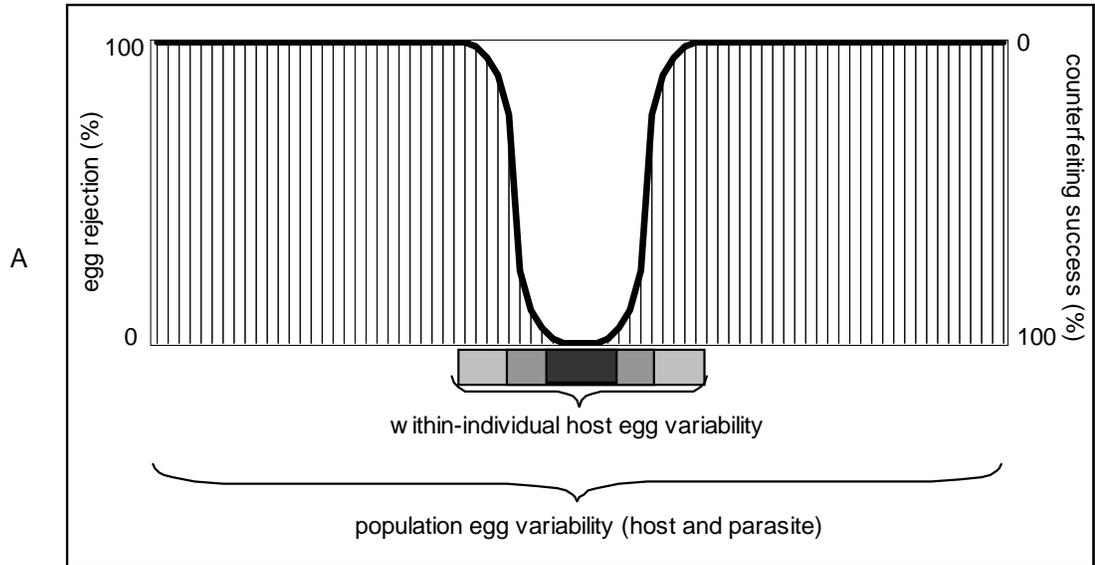
Descriptions in the left column are of the differences between host and experimental eggs. Data are from conspecific eggs from the Dominican Republic (63 cases in Cruz & Wiley (1989), and 78 cases in this study), and artificial eggs designed to look like village weaver eggs (49 cases in Cruz & Wiley (1989)). In both datasets, egg color differences between host and foreign eggs were random, but limited to 1/2 the population range. The degree of spotting of spotted experimental eggs was random, reflecting population variability.

**Table 7.3. Egg Rejection by Village Weavers in the Dominican Republic: Replication of Cruz & Wiley (1989)**

<b>Data from Robert &amp; Sorci 1999</b>				
	accepted	rejected	<i>N</i>	% rejection
eggs similar in color and spotting	21	4	25	16.0
eggs different in color and spotting	13	27	40	67.5
<b>Data from this study</b>				
	accepted	rejected	<i>N</i>	% rejection
eggs similar in color and spotting	31	3	34	8.8
eggs different in color and spotting	10	18	28	64.3

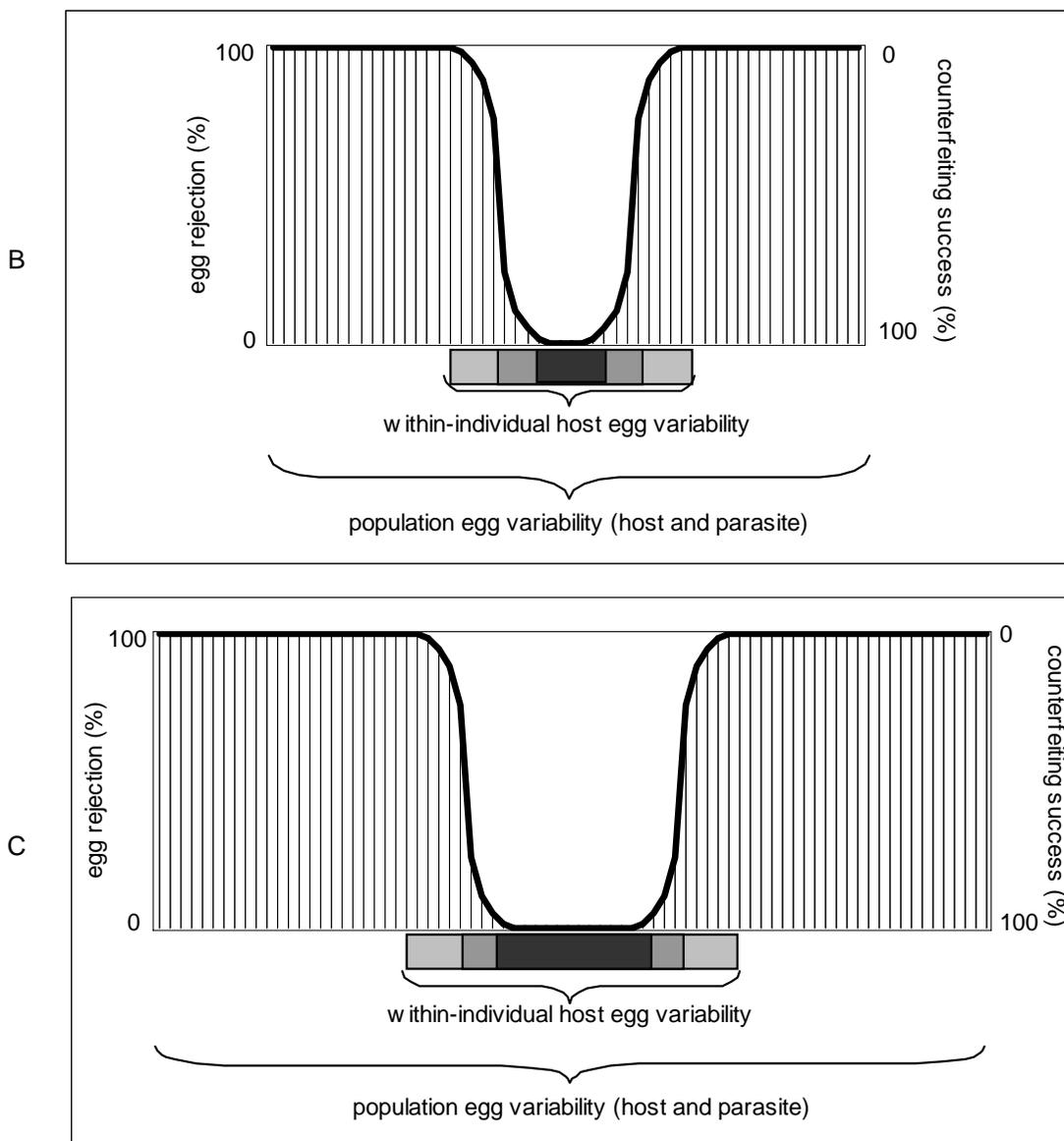
Descriptions in the left column are of the differences between host and experimental eggs. Data from Robert & Sorci (1999) are from artificial eggs designed to look like village weaver eggs; an artificial cowbird egg was also introduced with the artificial weaver eggs in many cases. Data from this study are from conspecific eggs, some of which were painted colors found among natural eggs in the Dominican Republic. The "similar" vs. "different" distinctions in Robert & Sorci (1999) and in this study were based on subjective estimations in the field. Robert & Sorci (1999) did not remove host eggs during the experiment, but one host egg was removed from each nest in this study.

**Table 7.4. Egg Rejection by Village Weavers in the Dominican Republic: Replication of Robert & Sorci (1999)**



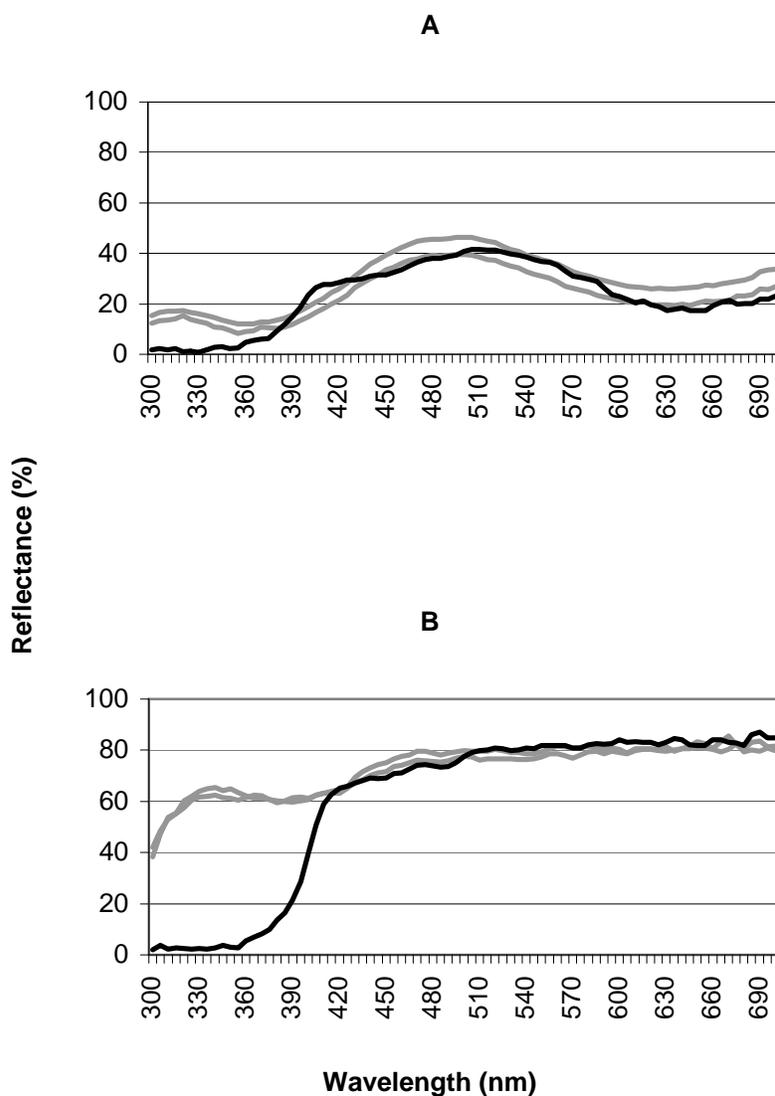
(A) relates egg rejection to parasite and host egg appearance variability for one parasite-host community. The population egg variability of the host and of the parasite are represented in one dimension (x-axis), assuming that the ranges are approximately equal. Egg variability is portrayed as continuous here but this is not necessary to the model. The shaded box beneath the graph is the range of egg variability in one host individual; one can imagine that there are as many boxes distributed along the x-axis as there are hosts in the population. Within-individual variation in cuckoo eggs is not considered here. The curve is rejection behavior (from the host's perspective, left y-axis) or success in mimicry or counterfeiting (from the parasite's perspective, right y-axis) for an egg of appearance  $x$ , given host rejection behavior. *Egg rejection efficiency* of a host is proportional to the ratio of the area below the curve (striped) to the area above the curve (clear). The host's interest is to maximize this ratio while avoiding the rejection of own eggs, in order to minimize counterfeiting success by the parasite. The parasite's interest is to minimize this ratio (to maximize the relative area above the curve), in order to maximize counterfeiting success over the range of host egg variability. Egg recognition ability is held constant in all panels of this model (see next page), so all change in egg rejection is due to accommodation to egg appearance changes. Change in egg recognition ability could be represented as a change in the shape of the curve relative to within-individual host egg variability, for example in the width of the parabolic portion (range of acceptance) or in the average slope (breadth of acceptance-rejection threshold).

**Fig.7.1. Graphical Model of the Relationship Between Egg Variability and Egg Rejection Behavior**



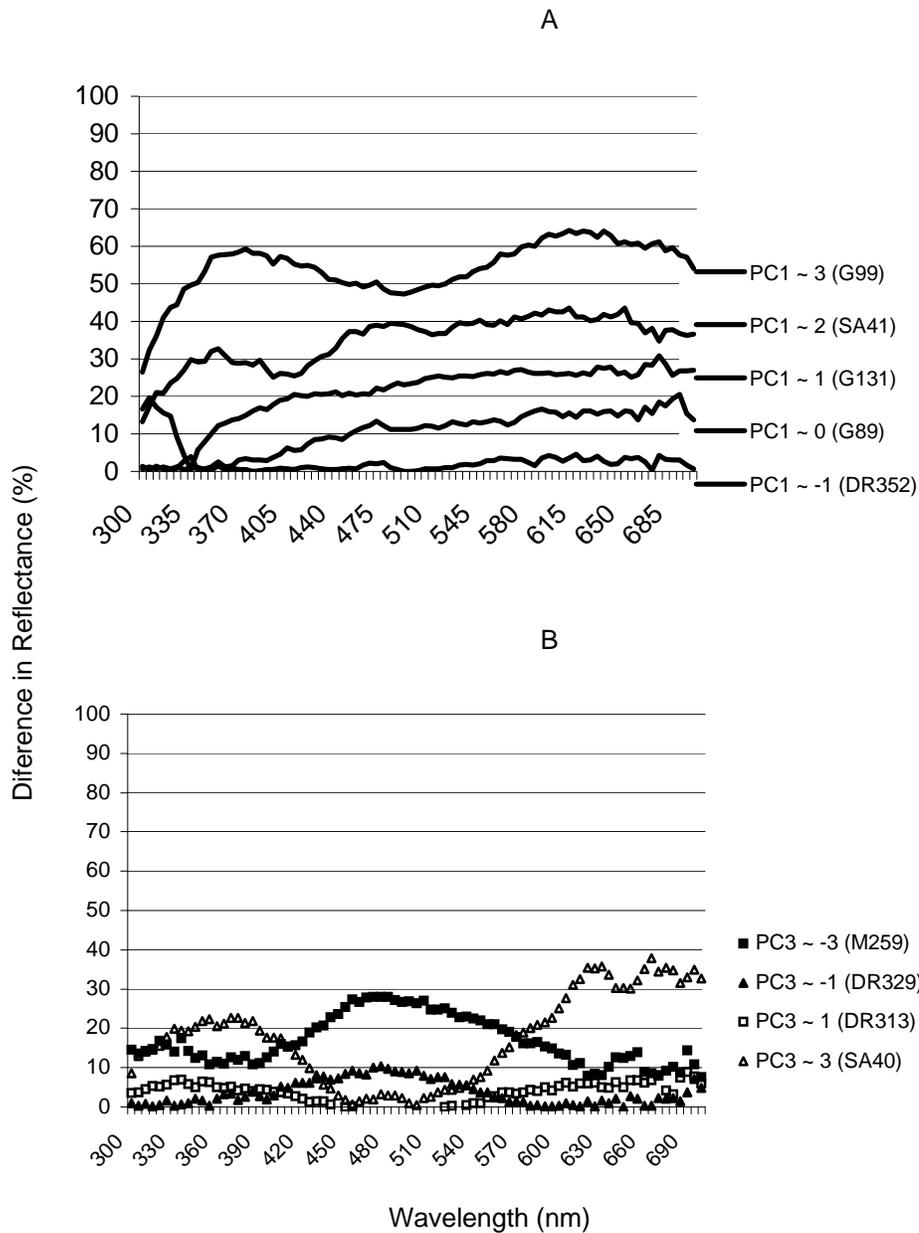
These two panels demonstrate evolution of egg rejection as a byproduct of egg variability in a population which has been removed from parasitism, if sympatry were to be reestablished. In the host population represented in (B), egg rejection efficiency (see caption to (A)) has decreased relative to that of (A) because host population variability has decreased. This negatively affects rejection efficiency by two means: more host egg ranges crowd over a smaller range of population egg variability, so a host will have a higher likelihood of laying eggs in the zone of any given parasite's highest success; and over evolutionary time, cuckoo egg variability should evolve to match that of the host, increasing the proportion of the parasite population that can successfully parasitize any given host. In (C), egg rejection efficiency has decreased relative to that of (A) because within-individual host egg variability has increased, increasing the counterfeiting success of the parasite over a greater range of egg variability.

**Fig.7.1. Graphical Model of the Relationship Between Egg Variability and Egg Rejection Behavior, continued**



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.

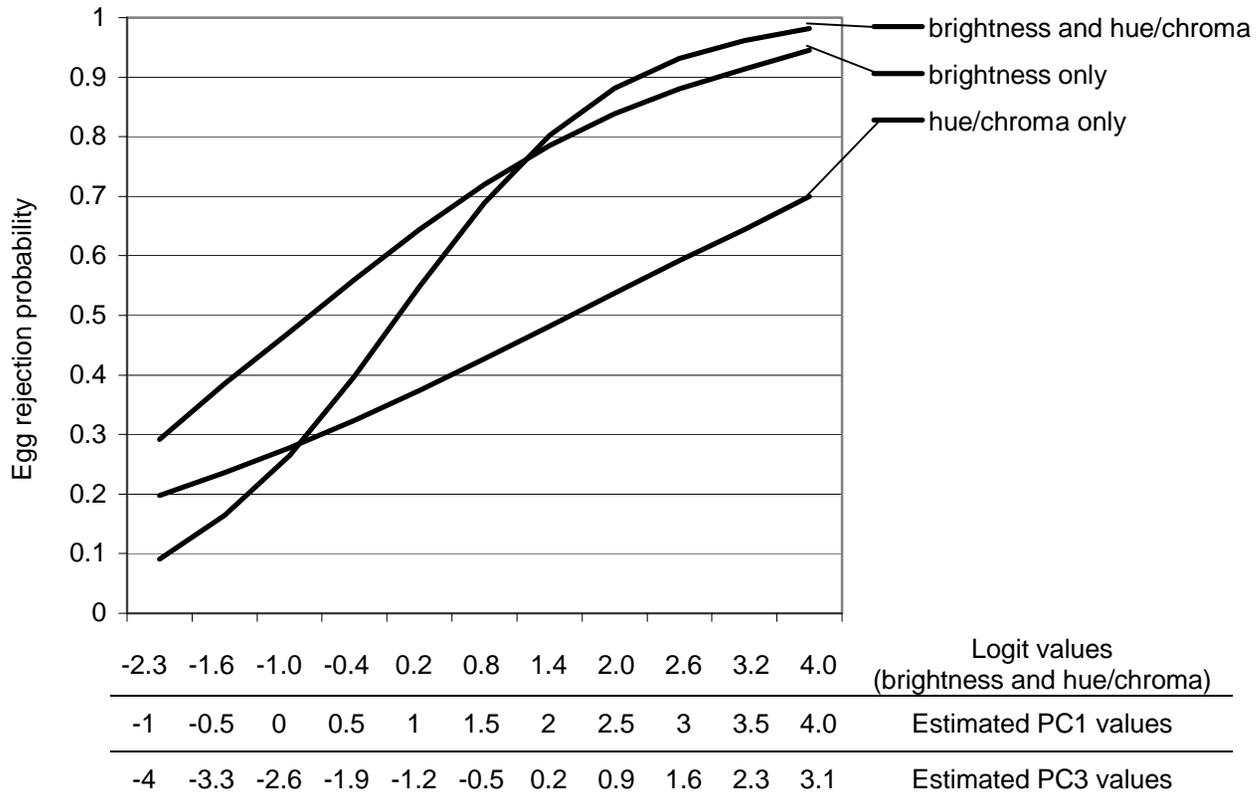
**Fig.7.2. Match of Paint to Actual Village Weaver Egg Colors (Spectra):  
(A) dark blue-green (control), (B) off-white**



In (A), the legend bars point to the respective spectral examples. As the PC1 value increases, the difference in average reflectance increases. According to the combined model (see Table 7.1), for each difference between two adjacent lines, average rejection probability increases by 88%.

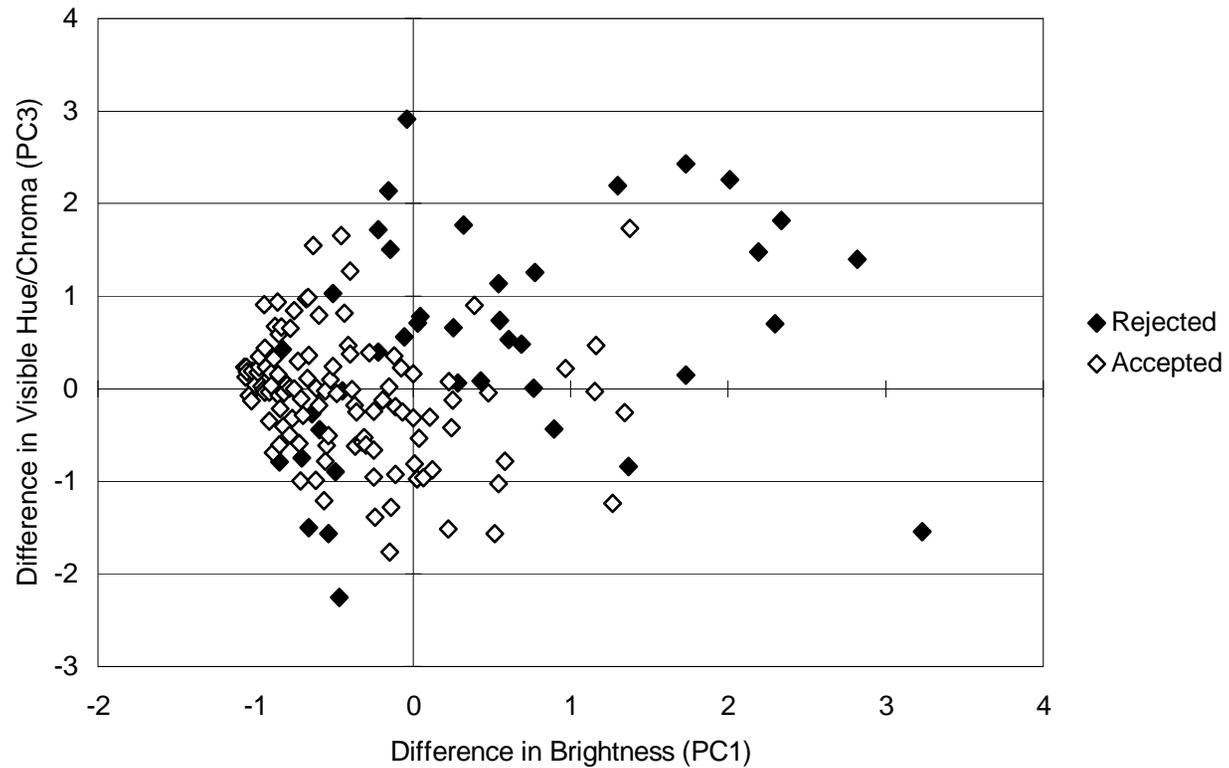
In (B), negative PC3 values (filled symbols) are concave down, i.e. maximum near 480 nm; positive PC3 values (open symbols) are concave up, i.e. minimum near 480 nm. The PC3 values here are two units apart. According to the combined model, then, for each difference between any two adjacent lines (in terms of PC3 values) average rejection probability increases by a factor of 2.43 (two increases of 56%).

**Fig.7.3. Relationship of (A) PC1 and (B) PC3 Values to Sample Spectral Differences Between Host and Experimental Eggs**



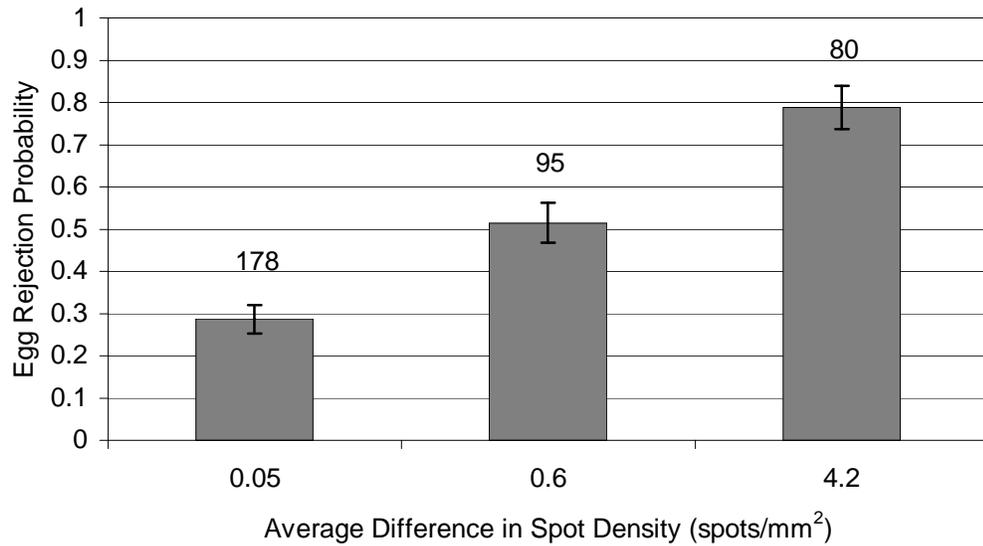
Each line is a logistic regression model based on the empirical data from all four populations combined. Logit values are based on the logistic regression model's integration of PC1 (brightness) and PC3 (hue/chroma). PC1 and PC3 values are distributed evenly across the x-axis.

**Fig.7.4. Village Weaver Rejection of Eggs by Difference in Color Between Host and Experimental Eggs: Logistic Regression Model**



Data are from all study populations. See Fig.7.3 for relation of PC values to mean reflectance differences. Eggs with spotting differences >1 in any category were excluded.

**Fig.7.5. Village Weaver Rejection of Eggs by Difference in Color Between Host and Experimental Eggs: Plot of Acceptances and Rejections in Color Difference Space**



Data are categorical, from all populations combined; quantitative values are estimates based on indexing (see Chapter 6: Methods, and Fig.6.6). 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 error.

**Fig.7.6. Village Weaver Rejection of Eggs by Difference in Spot Density Between Host and Experimental Eggs**

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## APPENDIX

### **Eigenvectors for Principal Component Analysis of Differences Between Host and Experimental Eggs**

The following table summarizes the reduction of 82 wavelength variables to four principal components. It is a list of the eigenvectors for the first four components of the PCA performed in Chapter 7, on the differences between host and experimental eggs. The variables in the left column are light wavelengths, and the values in each principal component column are the coefficients in the linear equation that forms that principal component (eigenvector). The magnitude of each coefficient therefore indicates the relative contribution of that wavelength to the principal component.

	PC1	PC2	PC3	PC4
W300	0.07749	-0.10613	0.11241	0.41096
W305	0.08121	-0.14647	0.10457	0.35271
W310	0.08834	-0.15415	0.08338	0.31160
W315	0.09003	-0.17156	0.07931	0.25981
W320	0.09099	-0.18356	0.06779	0.21965
W325	0.09218	-0.18634	0.05574	0.20558
W330	0.09181	-0.19530	0.05726	0.16675
W335	0.09400	-0.19893	0.04884	0.10592
W340	0.09351	-0.20772	0.03612	0.05455
W345	0.09233	-0.21486	0.03194	-0.00246
W350	0.09172	-0.21686	0.02408	-0.01494
W355	0.09147	-0.21617	0.01274	-0.05717
W360	0.08683	-0.22533	0.01233	-0.10320
W365	0.08457	-0.22870	0.01590	-0.12224
W370	0.08308	-0.22987	0.01541	-0.13665
W375	0.08171	-0.22627	0.01372	-0.17647
W380	0.07849	-0.22330	0.01914	-0.22041

W385	0.07820	-0.21645	0.02924	-0.24183
W390	0.08126	-0.19760	0.02804	-0.27053
W395	0.09262	-0.15893	0.01629	-0.26704
W400	0.10887	-0.09925	0.00034	-0.19680
W405	0.11832	-0.04216	-0.00729	-0.07551
W410	0.11964	-0.00426	-0.01262	-0.00765
W415	0.12019	0.01453	-0.00683	0.00154
W420	0.12044	0.02748	0.00409	0.00726
W425	0.12076	0.03396	0.02383	0.00084
W430	0.12170	0.03890	0.04823	-0.01008
W435	0.12117	0.04778	0.07481	-0.01196
W440	0.12045	0.05158	0.09759	-0.02919
W445	0.11888	0.05593	0.12246	-0.03405
W450	0.11710	0.05926	0.14372	-0.03960
W455	0.11554	0.06660	0.15277	-0.03895
W460	0.11334	0.07049	0.16663	-0.05171
W465	0.11236	0.07713	0.17367	-0.04916
W470	0.11185	0.08024	0.17715	-0.04787
W475	0.11106	0.08450	0.17914	-0.04920
W480	0.11082	0.08492	0.18147	-0.05443
W485	0.11087	0.08578	0.18298	-0.05029
W490	0.11101	0.08674	0.18164	-0.05068
W495	0.11151	0.08954	0.17654	-0.04339
W500	0.11293	0.09570	0.15726	-0.02322
W505	0.11373	0.09773	0.14368	-0.01110
W510	0.11457	0.09789	0.13002	-0.00168
W515	0.11520	0.09752	0.11951	-0.00047
W520	0.11591	0.09576	0.10948	0.00511
W525	0.11694	0.09351	0.09601	0.00365
W530	0.11747	0.09054	0.08893	0.00298
W535	0.11819	0.08786	0.07741	0.00740
W540	0.11931	0.08385	0.05625	0.00923
W545	0.12026	0.07870	0.04307	0.00566
W550	0.12067	0.07733	0.02109	0.01416
W555	0.12125	0.07156	0.00024	0.01233
W560	0.12174	0.06549	-0.01867	0.00867
W565	0.12196	0.06050	-0.03452	0.01672
W570	0.12216	0.05491	-0.04990	0.01397
W575	0.12217	0.04950	-0.06387	0.00682
W580	0.12204	0.04651	-0.07868	0.00417
W585	0.12165	0.04591	-0.08410	0.00995
W590	0.12153	0.04163	-0.09218	0.00862
W595	0.12148	0.03688	-0.10286	0.00799
W600	0.12072	0.03655	-0.11863	0.01339

W605	0.12040	0.03086	-0.12987	0.00569
W610	0.12000	0.02612	-0.13801	0.01020
W615	0.11975	0.02212	-0.14442	0.01099
W620	0.11921	0.02014	-0.15265	0.00788
W625	0.11892	0.01816	-0.15666	0.00145
W630	0.11883	0.01992	-0.15610	0.00869
W635	0.11875	0.02399	-0.15444	0.01120
W640	0.11939	0.02285	-0.14739	0.00726
W645	0.11978	0.01847	-0.14138	-0.00061
W650	0.11971	0.01700	-0.14221	0.00101
W655	0.11879	0.01787	-0.15356	0.00557
W660	0.11845	0.02519	-0.15849	0.01836
W665	0.11724	0.02295	-0.16857	0.01382
W670	0.11749	0.02374	-0.16260	0.01423
W675	0.11737	0.01810	-0.15766	0.00767
W680	0.11829	0.01758	-0.15060	0.01408
W685	0.11805	0.03033	-0.14114	0.03846
W690	0.11645	0.03604	-0.14464	0.03291
W695	0.11611	0.03643	-0.13483	0.04154
W700	0.11700	0.03963	-0.13368	0.03665