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INHERITANCE OF EGG-COLOR POLYMORPHISM IN THE VILLAGE WEAVER (*PLOCEUS CUCULLATUS*)

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ABSTRACT.—Eggs collected from an aviary colony of Village Weavers (*Ploceus cucullatus cucullatus*) over a 14-year period varied in color among different females from white to emerald or turquoise, and from many spots to few or none. Color and amount of spotting of the eggs of a given female were constant throughout her life (based on 815 eggs from 37 females). Color was judged from the *Villalobos Color Atlas*. Mendelian analysis of five different hypotheses showed that inheritance of background color of eggs in 20 different crosses was consistent only with a hypothesis of two independent pairs of autosomal alleles for hue. Received 14 September 1992, accepted 25 November 1992.

THE EDITORS of a recent book on avian genetics pointed out that, despite widespread interest among ornithologists in plumage polymorphism, evidence of the genetic basis for most of these polymorphisms is sadly lacking (Cooke and Buckley 1987:202). Even less is known about the genetic control of egg-shell-color polymorphisms. My objective is to present evidence on Mendelian inheritance of egg-shell-color polymorphism in a passerine bird. In the domestic fowl (*Gallus gallus*) for which the first demonstration of Mendelian heredity in the animal kingdom was made by William Bateson (Punnett 1923), a Mendelian analysis of egg-shell-color polymorphism was done long ago (Punnett and Bailey 1920, Punnett 1923, 1933a), and this classic work is still one of the few published records dealing with this problem (Washburn 1990). There is no reference in the literature giving comparable evidence for any passerine bird.

In North America the color of eggs is gen-

erally consistent for a given species of bird, and this is particularly true of the passerines (Harrison 1978). This is in strong contrast to the genus *Ploceus* (Ploceidae, weaverbirds) in which variation in egg color within the species is higher than in any other group of birds (Moreau 1960:446).

In the Village Weaver (*Ploceus cucullatus*) of sub-Saharan Africa, the eggs are among the most variable in color and pattern of any ploceid species (Meise 1983:521). The different races of the Village Weaver have similar variations in egg color and pattern, in which ground color varies from white through blues to greens, and from plain eggs to eggs spotted to varying degrees usually with brown or reddish brown. This pattern of variability is seen in eastern (Mackworth-Praed and Grant 1960), central (Chapin 1954), western (Bannerman 1949), and southern (Maclean 1985) Africa.

Bannerman (1949:94) further noted for the Village Weaver: "Only one type of coloring ap-



FRONTISPIECE. Upper panel illustrates the range of variation in color and pattern of eggs of the African Village Weaver (*Ploceus cucullatus*). Lower panel shows the four main background hues (from left to right); emerald, emerald turquoise, turquoise, and white. Eggs of each hue may or may not be spotted. Photographs by Nicholas E. Collias.

pears in each nest and the diversity exhibited may be a provision of Nature to enable a colonial nesting species to recognize its own eggs." Inspection of many clutches in museums suggests that each individual female in different species of plover weaver may lay her own characteristic color and pattern of eggs (Meise 1983:521).

The multiplicity of egg-color types in the Village Weaver raises two interesting questions: (1) Does a given female always lay the same type of egg, or does it vary from time to time? (2) If egg type is consistent, is it inherited and, if so, what is the mode of inheritance?

Observations over several years of Village Weavers of the western African subspecies (*P. cucullatus cucullatus*) breeding in large aviaries showed clearly that each female has her own particular combination of color and pattern, and consistently lays one type of egg, no matter how much the different females may differ in egg type (Victoria 1969, 1972, Collias and Collias 1970). In fact, continued observations over a long period of time have shown that each female lays her own characteristic type of egg over her entire lifetime (Collias 1984).

The frontispiece illustrates the great range of variation in color and pattern of eggs of the Village Weaver, including the four types of hue in background coloration reported here. A recent general account of bird eggs by Kiff (1991) has excellent color photographs by Clark Sumida illustrating variation in color and pattern of eggs among several species of birds noted for variable eggs, among them the Village Weaver (Black-headed Weaver).

MATERIALS AND METHODS

The Village Weaver is a colonial, polygamous species that breeds over most of Africa south of the Sahara. The breeding habits of these birds and their long life span (Collias 1984, Collias et al. 1986) made it possible not only to obtain eggs from several clutches in the same year, but also eggs over several years from matings with different males. A female may or may not choose the same male for each subsequent brood.

The eggs used in this study came from our breeding colony of Village Weavers (*P. c. cucullatus*) at the University of California, Los Angeles and were collected over 14 years (Collias 1984). N. Collias and I and our associates were doing other experiments during this period that required the females to make a choice among the nests built by the males. To maximize the

number of choices, we removed the eggs within one or two days after the eggs were laid. Each of the eggs was identified as to the female that laid it and the date of laying of the first egg of the clutch. There are two or three eggs in a clutch.

A record was also kept of the male with whom the female was mated at that time. We consider the observed parentage of the eggs generally to be reliable since, out of hundreds of copulations observed in the field and in our aviaries, extrapair copulations were extremely rare. In a seven-month field study of one colony of Village Weavers in central Africa (Collias and Collias 1959) only one extrapair copulation was seen. During four years of observation in one of our aviaries, Victoria (1969:20) observed two cases. Both occurred when two females accepted the same nest and both started to copulate with the male who owned the nest. But by the following day, the subordinate female had left that male's territory and started to copulate with another male in whose nest she laid her clutch. Instances of a female laying an egg in another female's nest were very rare and, furthermore, a female Village Weaver will throw eggs out of her nest when they do not match her own (Victoria 1972).

Color, degree of spotting, length and width were determined for 815 eggs from 37 females. These eggs are deposited in the Western Foundation of Vertebrate Zoology, Camarillo, California. In general, these eggs represented samples over the entire lifetime or most of the lifetime of these females. The *Villalobos Color Atlas* (1947), which contains 7,279 colors, was used to determine the color of each egg. This color atlas is the one adopted for use in the *Handbook of North American Birds* (Palmer 1962:4) because it has a sound theoretical basis, it is a workable universal standard, and the color terms are widely meaningful.

The atlas divides the spectrum into 33 hues, hue being that quality which permits one to differentiate one color of the spectrum from another. On a separate page for each hue there are 191 variations of that hue plus a series of neutrals ranging from black to white. These 191 variations are based on: (1) lightness, which is that property that distinguishes one color from another as being lighter or darker regardless of hue; and (2) chromaticity, the property of a color that denotes whether the hue is more or less attenuated, regardless of whether the color is light or dark (i.e. chromaticity varies with concentration of color pigment). The lightness scale has 21 grades, corresponding to a neutral gray series from (0) black to (20) white. The chromaticity scale has 12 grades ranging from (1) extreme attenuation to (12) no attenuation.

The ground color of the egg shells of the Village Weaver varied in hue from white through turquoise to emerald turquoise, emerald and emerald green. The amount of spotting was classified into three grades: (1) 0, no spotting or so little as not to be noticeable unless examined very closely; (2) +, a small amount

TABLE 1. Number of eggs of female *Aba* in various categories of egg color and spotting. Based on eggs laid in nine different years. All of turquoise hue.

Lightness ^a		Chromaticity ^b		Spotting ^c	
Grade	No.	Grade	No.	Amount	No.
0-14	1	0-1	0	0	59
15	2	2	2	+	0
16	8	3	0	++	0
17	43	4	9		
18	5	5	10		
19-20	0	6	32		
		7	5		
		8	1		
		9-12	0		

^a Lightness grades 0-20 (black to white).

^b Chromaticity grades 0-12 (from greatest to least attenuation of hue).

^c Spotting based on three arbitrary grades: 0 (absence of spotting), + (little spotting), ++ (considerable spotting).

of spotting with the spots relatively small and uniformly distributed; and (3) ++, considerable spotting, often with blotches, which might be concentrated in one area. Spotted eggs always had brown spots; however, the eggs of some females also had very pale lavender spots. The spotting categories were coarser and more subjective than those for egg color.

The complete genealogy of all the birds in our colony was recorded, except for the founders. A pedigree analysis was undertaken in an attempt to recognize Mendelian factors that control the ground color or hue of the eggs. The methods followed were similar to those used in human-pedigree analysis (Crow 1966, Rothwell 1977), as well as that used by Punnett (1923, 1933a) in his Mendelian analysis of the genetics of egg color in domestic fowl. This mode of analysis is also consistent with more recent accounts of Mendelian heredity in the domestic fowl (Crawford 1990, Stevens 1991). Cooke and Buckley (1987:31-32) suggested some useful guidelines for performing Mendelian genetic analyses on wild birds in field and aviary.

RESULTS

The data demonstrated that, although all of the eggs laid by a given female are not identical in one or more of the four categories used to characterize the color and pattern of a given egg (hue, lightness, chromaticity and spotting), the differences may well not be noticeable without quantification. An example of this consistency is given in Table 1, showing the variation in 59 eggs of female *Aba* laid over a period of nine years. Each egg was characterized by the mode for each of the four categories. Female *Aba*'s eggs, consequently, are of turquoise hue,

TABLE 2. Modes of egg colors for 37 female Village Weavers.

Female	No. eggs	Hue ^a	Lightness	Chromaticity	Spotting
BA	19	E	15	5	++
PB	19	W	20	0	+
GW	13	ET	17	3	++
WW	11	T	17	4	0
APn	12	T	18	4	+
AA	13	ET	17	2	++
Bwr	14	T	18	3	0
Rwr	17	ET	17	5	++
WA	34	ET	17	3	++
YR	19	ET	19	1.5	++
Oar	55	W	19	0	+
Aba	59	T	17	6	0
AO	17	ET	17	4	0
Ara	13	E	16	4	++
Aya	65	ET	18	4	++
Bab	6	W	20	0	++
Brg	15	T	18	2	++
GG	20	ET	17.5	2	++
Gwb	37	E	15	4	++
Oba	11	E	16	4	++
OO	22	E	16	4	++
Wba	8	ET	16.5	3	++
Yro	24	T	18	2	++
Rya	18	E	18	4	++
Rab	6	W	19	0	++
AB	31	ET	15	2	++
LW	22	E	14	4	++
RY	44	ET	14	2	++
YB	31	W	20	0	+
GY	31	ET	15	1	++
LG	8	ET	14	6	0
OL	16	W	16	0	++
RG	34	ET	15	1	+
YL	38	W	17	0	0
YY	7	T	14	2	++
Wrw	2	W	20	0	++
Bya	4	ET	14	3	0

^a (W) white; (T) turquoise; (ET) emerald turquoise; (E) emerald.

lightness grade 17, chromaticity grade 6, and unspotted. Table 2 gives the modal values in these egg characteristics for 37 female Village Weavers, and shows the pronounced way in which females differ in the type of egg they lay. These modal values are consistent for each female throughout her lifetime (Collias 1984).

No female in our colony had a modal hue of emerald green. In fact, emerald-green eggs occurred in only six females and, usually, this color was found in no more than four eggs for a given female. None of the offspring or mothers of these females had emerald-green eggs. Thus, it was impossible to determine the in-

TABLE 3. Segregation patterns in Village Weavers on hypothesis of two alleles at two independent autosomal loci for egg background color. Daughters' eggs were consistent with this hypothesis for all crosses. Inferred genotypes in parentheses. Phenotypes as specified for egg color: (E) emerald; (T) turquoise; (ET) emerald turquoise; (W) white.

Matings	No. daughters with their egg color				Notes on genealogy
	E	T	ET	W	
1 ♂ AW (EeTt) × ♀ PB (eett), W		2	1		♂ AW, ♀ PB, original stock.
2 × ♀ Lbw (e-t) ^a		1			♀ Lbw daughter of ♀ PB, W.
3 × ♀ GW (EeTt), ET			3	1	♀ GW daughter of ♀ WB (egg hue unknown).
4 × ♀ WA (E-Tt), ET	1				♀ WA daughter of ♀ GW, ET and of ♀ AW her mate here.
5 ♂ RA (e-Tt) × ♀ BA (Eett), E	2	1		2	♂ RA, ♀ BA, original stock.
6 × ♀ AA (E-Tt), ET	1				♀ AA daughter of ♀ GW, ET and granddaughter of RA.
7 ♂ Awr (EeTt) × ♀ WA (E-Tt), ET			1		♂ Awr son of ♀ PW (egg hue unknown). ♀ WA daughter of ♀ GW, ET.
8 × ♀ Oar (eett), W			1		♀ Oar daughter of ♀ PB, W.
9 × ♀ Aba (eeTt), T			1	1	♀ Aba daughter of ♀ PB, W and half-sister of ♀ Oar.
10 ♂ AB (E---) × ♀ WW (eeT-), T			1		♂ AB, original stock. ♀ WW daughter of ♀ PW (egg hue unknown).
11 × ♀ Bwr (eeTt), T			1		♀ Bwr daughter of ♀ PB, W.
12 ♂ Yrb (E-t-) × ♀ Brg (eeTt), T	1				♂ Yrb son of ♀ BA, E and brother of ♂ AR. ♀ Brg daughter of ♀ Lbw ^a (e-t-).
13 ♂ AR (E---) × ♀ Brg (eeTt), T			1		♂ AR son of ♀ BA, E and brother of ♂ Yrb. ♀ Brg (see 12).
14 ♂ YY (----) × ♀ Rwr (E-T-), ET			2		♂ YY, original stock. ♀ Rwr daughter of ♀ GW, ET.
15 ♂ WB (e-t-) × ♀ RY (EeTt), ET				1	♂ WB son of ♀ Wba, ET. ♀ RY daughter of ♀ AA, W.
16 ♂ Brb (e-t-) × ♀ Oar (eett), W				1	♂ Brb son of ♀ Lbw half-sister of ♀ Oar daughter of ♀ PB, W.
17 ♂ Yra (----) × ♀ Wba (EeT-), ET			1		♂ Yra son of ♀ AA, ET. ♀ Wba daughter of ♀ WW, T.
18 ♂ BW (--t-) × ♀ Rwr (E-Tt), ET	1				♂ BW original stock. ♀ Rwr daughter of ♀ GW, ET.
19 ♂ WY (e-t-) × ♀ PB (eett), W				1	♂ WY son of ♀ PW (egg hue unknown). ♀ PB, original stock.
20 ♂ Wbr (e---) × ♀ AB (EeT-), ET		1			♂ Wbr son of ♀ GW, ET. ♀ AB daughter of ♀ GW, ET.

^a No eggs recorded for ♀ Lbw; part of her genotype (e-t-) deduced from her mother ♀ PB (eett).

inheritance of this color, or even if it was inherited and not due to some external factor.

My findings are based on 20 crosses (pairings), involving 13 males and 15 females, that resulted in at least one daughter from which eggs were also obtained. All clutches of a given pair are pooled as one cross. Crosses involved a number of different combinations that facilitated the genetic analysis of egg-color inheritance. For different broods individual males mated with from one to four females, and the females mated with from one to three males. In addition, some of the crosses involved birds that we knew were related, such as father and daughter, grandfather and granddaughter, aunt and nephew, and two brothers that mated with

the same female. All of the females can be traced back to four original females, two of which are included in this analysis. The other 35 females were one to four generations removed from the original females.

Five different genetic hypotheses were tested for egg-shell-color polymorphism in the Village Weaver. The simplest explanation (hypothesis 1) for the inheritance of egg color is that of one locus and two alleles. This system predicts only three phenotypes, but four were observed: emerald (E), turquoise (T), emerald turquoise (ET), and white (W). Therefore, it was rejected. Three other alternative hypotheses were also evaluated and rejected: (hypothesis 2) that there were three alleles at one locus (E,

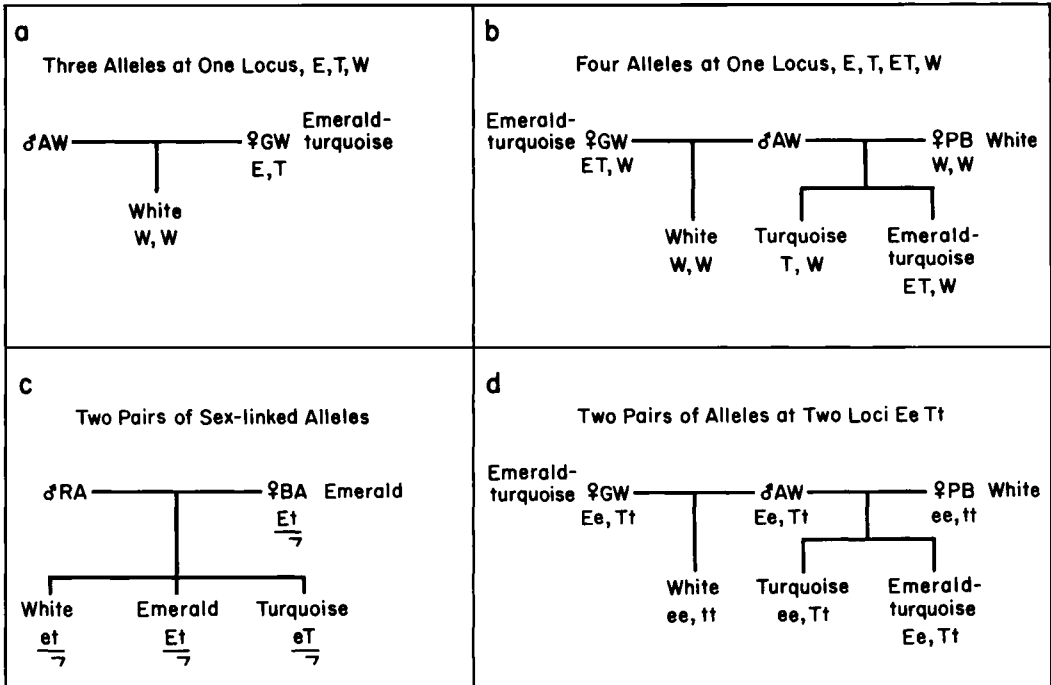


Fig. 1. Examples of matings in Village Weaver with color of eggs laid by daughters. Four hypotheses for inheritance of egg-shell color (ground color) compared. Data do not fit hypothesis that egg-shell color is due to (a) three or (b) four alleles at one locus, nor do they fit hypothesis (c) that egg-shell color due to two pairs of sex-linked alleles. However, data are consistent with hypothesis (d) of a pair of alleles at each of two autosomal loci, with turquoise allele and emerald allele dominant over white allele, but not over each other (emerald-turquoise egg).

T, and W, with white only in a homozygous individual); (hypothesis 3) that there were four alleles at one locus (E, T, ET, W); and (hypothesis 4) that there were two pairs of alleles, both of which are sex-linked. To test these alternative hypotheses, I again checked actual crosses.

To evaluate the validity of hypothesis 2 (three alleles at one locus), I used the cross (Table 3, mating 3) between male AW and female GW (ET phenotype) that would have a genotype of ET for her emerald-turquoise eggs with an E on one chromosome and T on the other (Fig. 1a). Their daughter laid white eggs (WW genotype). From this one can see that regardless of what the genotype of male AW might be, female GW could not have had a daughter that laid white eggs, since female GW could only contribute an E or a T to her daughter, who would then have to lay colored eggs.

Again, under the three-allele condition (hypothesis 2), white (w) would be recessive to both emerald (E) and turquoise (T). Female PB (white eggs; Table 3, mating 19) had a daughter

that laid all white eggs. However, mating 15 (Table 3), in which a male was mated to an ET female, like mating 19, produced one daughter that laid white eggs. Male AW, mated (Table 3, mating 1) with a white female (PB), produced daughters that laid turquoise or emerald-turquoise eggs. These matings clearly rule out inheritance by three alleles at a single locus.

I used the same birds to test hypothesis 3, that of four alleles at one locus, these alleles being E, T, ET, and W (Fig. 1b). In this case (Table 3, mating 3) it would be possible to get a daughter with white eggs if female GW had a genotype ET, W and male AW had genotype W-. I then checked the cross (Table 3, mating 1) of male AW with female PB, which laid white eggs and, therefore, theoretically had genotype WW. Since Female PB could furnish only W genes and male AW was shown to carry one W gene from mating 3 (Fig. 1a), color present in their daughters' eggs had to come from the other gene of male AW. This latter pair had three daughters, two of whom laid turquoise eggs (T-), and the other,

emerald turquoise (ET-). This is obviously impossible, since male AW could have had either a T or an ET gene but not both.

The possibility of the occurrence of two pairs of sex-linked alleles (hypothesis 4) was tested by the cross of male RA (Table 3, mating 5) with female BA, who laid emerald eggs (Et; Fig. 1c). The female in birds is the heterogametic (ZW) sex and so carries only one (W) chromosome, which corresponds to the Y-chromosome in mammals and in *Drosophila* (Stevens 1991). This pair had three daughters, one of whom laid white eggs (et), another, emerald (Et), and a third, turquoise (eT). If we assume male RA is heterozygous for both pairs of alleles, he could have two of the following combinations of genes: for colors ET, eT, Et, or et. His daughters had three of the possible combinations, but male RA could have only two. Hence, this explanation is not valid.

The last supposition (hypothesis 5) tested involved one pair of alleles at each of two autosomal loci on different chromosomes. The data are consistent with this hypothesis. One locus is for emerald (E) and the other for turquoise (T). These two colors result when one locus carries a dominant allele for its color, and the other is homozygous for the recessive (nonpigment) allele. Thus, a female laying emerald eggs would have a genotype of EEtt or Eett, and one laying turquoise eggs, eeTT or eeTt. A double-recessive female (eett) lays white eggs. A female who carries at least one dominant gene at both loci (E-T-) lays eggs that are a blend of the two colors (viz. emerald turquoise).

Using hypothesis 5 (two independent pairs of alleles at two autosomal loci), it can be seen that all 20 crosses were consistent with this hypothesis. An example of an actual cross that fits this hypothesis is shown in Figure 1d. Male AW mated with two females. Female GW laid emerald-turquoise eggs, so she had to have at least one dominant gene at both loci; however, since her daughter laid white eggs (genotype eett), female GW also had to have a recessive gene at each locus, as should male AW. Female PB laid white eggs (eett), but she had three daughters, two of which laid turquoise eggs (eeT-), and the third emerald-turquoise eggs (E-T-). Therefore, male AW, who we know from the first cross had to have a recessive gene at each locus (since he had a daughter that laid white eggs), also had to have a dominant gene at each locus

in order to furnish the E and T genes to his daughters by female PB.

The color of the mother's eggs was known for five of the males listed in Table 3. Female BA (emerald eggs) was the mother of male Yrb and male AR. Three other mothers had emerald-turquoise eggs. Listed (with their sons in parentheses) they were: WbA (WB), AA (Yra), and GW (Wbr). At least a partial genotype had been previously inferred for three of these males (Yrb, AR, and WB) from the egg colors of their daughters and their mates. These partial genotypes are consistent with hypothesis 5 of two alleles at each of two autosomal loci (Table 3).

The lightness values for the eggs range from 11 to 20 (all on light side) and the chromaticity values from 0 to 8. The data are not sufficient to determine the inheritance involving so many possible combinations, nor are the data sufficient to determine the inheritance of spotting, which also includes a large variety of conditions (i.e. amount of spotting, size of spots, location and arrangement of spots on egg). Each of the properties—spotting, chromaticity and lightness—is probably due to many factors, as are the measurements of length and width, which are quite consistent for a given female and vary significantly between females (Collias 1984).

DISCUSSION

Genetics of egg-shell-color polymorphism and associated pigments.—Because of the paucity of literature on the genetics of egg-color morphs for wild birds, one comes inevitably to domestic-fowl studies, which serve as guides to the possibilities and complexities of the situation. This literature has recently been summarized by Washburn (1990:796-797). The classic analysis of egg-shell-color polymorphism in the fowl by Punnett is summarized in his book on *Heredity in Poultry* (1923). Generally, the color of the egg shell in chickens varies from white to a dark brown, but it may rarely be blue or greenish, as in eggs laid by hens of the Araucano breed of domestic fowl in Chile. Mendelian analysis of this trait first performed by Punnett (1933a) indicated that the blue-egg character state behaves as a simple autosomal dominant to non-blue. The gene for the blue egg has now been located on a particular autosomal chromosome (Stevens 1991:280). Combined with various

shades of brown the gene for blue gives a series of greens and olives (Punnett 1933a).

The shades of brown in hens' eggs depend upon several genetic factors; the deepest brown results when the bird is homozygous for one major factor, as well as for minor factors. In some breeds an inhibitor factor dilutes the colors of the brown series so that what would be a deep-brown egg becomes pale brown (Punnett and Bailey 1920, Punnett 1923). Some of the genes for brown shell color may be sex linked (Hall 1944). Shoffner et al. (1982) have reported a recessive sex-linked mutant gene, which results in a lack of brown pigment in the shell from hens with the polygenic brown shell color.

The genes involved in color polymorphism must exert their influence via enzyme systems that produce the different pigments of the egg shell. Chemically, the egg-shell pigments are pyrrole derivatives (Burley and Vadehra 1989: 32) and products of the breakdown of hemoglobin (Romanoff and Romanoff 1949:227). The same pigments are widespread. Kennedy and Vevers (1976), in a survey of avian egg-shell pigments from 108 species, found that 100 species contained protoporphyrin, 52 had biliverdin IX α , 19 contained this biliverdin plus its zinc chelate, and 5 had no pigment. Many of the eggs contained more than one of these different pigments. Protoporphyrin tends to give brownish shell colors, and the biliverdins provide blues and greens (Burley and Vadehra 1989: 33).

Kennedy and Vevers (1973) also did a chromatographic analysis of the egg-shell pigments of the Araucano fowl, finding that these egg shells contained protoporphyrin, biliverdin IX α and its zinc chelate, and traces of coproporphyrin I. These eggs vary in color, especially through various shades or tints of blue and green. The absorption spectra of different fractions showed the basic color differences: deep pink for the fraction identified as protoporphyrin, deep greenish-blue for the biliverdin IX α fraction, and bright emerald-green for the pigment chemically identified as the zinc chelate of biliverdin IX α . Considering the general distribution and limited number of avian egg-shell pigments, the biliverdin pigment might be controlled in whole or part by a gene for blue-green color in the turquoise egg of the Village Weaver, and the zinc chelate of this biliverdin pig-

ment by a gene for green color in the emerald egg of this species. In general, eggs of the Village Weaver do not have a brownish ground color, such as might be due to protoporphyrin.

Punnett (1933a) in his article on genetics of the blue egg had an excellent color plate (no. XXII) illustrating polychromatism in six eggs of different colors in the domestic fowl. I compared the "blue" egg on his color plate with the *Villalobos Color Atlas*; this blue egg is definitely pale blue-green (i.e. "turquoise").

The ground color of egg shells is due to pigment in the calcareous layer, while spots and other markings are deposited afterward in the cuticle or on the surface of the egg (Romanoff and Romanoff 1949:172 and 227, Baird et al. 1975). Often Village Weaver eggs, whether white or colored, are more or less spotted. Initially, it seemed to me that presence or absence of spotting might be consistent with a hypothesis of one major pair of autosomal alleles, but in view of the very great variability in amount, distribution, and type of spotting, it is likely that polygenic control is involved. Usually, the spots are brown or reddish brown in eggs of the Village Weaver. Kennedy and Vevers (1976) in their sample of avian egg-shell pigments in many species stated that the markings on egg shells (various shades of brown) were invariably due to protoporphyrins. It seems likely, therefore, that the same is generally true of brown or reddish-brown spots in Village Weaver eggs. As indicated the evidence from chicken eggs suggests that brownish egg-shell ground color is under polygenic control, and this could well be true of brownish spotting as well.

In the weaver genus *Ploceus*, with approximately 60 species (Moreau and Greenway 1962), white and bluish or blue-green eggs are common, and green eggs less so, while brown as a ground color for the egg shell of different species is least frequent (Mackworth-Praed and Grant 1960, 1963, 1973, Meise 1983:519-521). Completely brown eggs, along with other color morphs, occur widely over Africa among a few weaver species. For example, the Niger Black-headed Weaver (*P. capitalis*) of western Africa (Bannerman 1949), the Brown-throated Weaver (*P. xanthopterus*) of southern Africa (Maclean 1985), and the Northern Masked Weaver (*P. taeniopterus*) of eastern Africa (Jackson 1990) lay chocolate-brown or dark brown eggs, among other color types. The wide differences in egg-

shell pigmentation among species of *Ploceus* must reflect corresponding differences in frequencies of the genes that produce the enzymes controlling the egg-shell pigments.

The eggs of individual European Cuckoos (*Cuculus canoris*) often closely match those of the particular foster species in color and pattern; different hosts' eggs may even be mimicked by different cuckoos in the same locality (Davies and Brooke 1991). Punnett (1933b) suggested a genetic theory for cuckoo-egg mimicry, namely, the location of a series of multiple allelomorphs for egg color and pattern on the Y-chromosome (now known as the W-chromosome in birds). Under this hypothesis every daughter of a female cuckoo would resemble her mother in the character of the eggs, no matter who her father was. Jensen (1966) reviewed the evidence and favored Punnett's hypothesis but, like Wickler (1968:198), pointed out that it remains to be tested cytologically and genetically. Apparently, there is still not sufficient evidence.

Natural selection for egg-shell-color variability.— It has been shown that many species of birds will eject dissimilar eggs placed in their nests (Victoria 1969, 1972, and see below). The evolution of egg-shell-color polymorphism has been explained by theories involving conspecific or interspecific nest (brood) parasitism. These two theories are not necessarily alternatives and both types of explanation could be involved for the same species.

Victoria (1969, 1972) observed that a female Village Weaver may rarely lay in the nest of another female Village Weaver, particularly when available nests were in short supply. Victoria observed the birds for 2 h a day, five mornings a week, over a four-year period in our breeding colony of Village Weavers (originally from Senegal) in large outdoor aviaries in southern California. In extensive experiments Victoria (1969, 1972) found that a Village Weaver female will reject dissimilar eggs of other female Village Weavers when these eggs are placed in her nest, but she will accept an egg that closely resembles her own. This behavior provides a selection pressure for high egg variability between clutches of different individual females, but for low egg variability within clutches of the same female. In three-egg replacement experiments where the host's own egg was the odd one, it was the only egg not rejected, indicating that egg color and pattern, rather than oddity, are what the birds recog-

nize. Experiments on rejection or acceptance of eggs also showed that the presence or absence of spots played a more important role when the difference in ground color of eggs was small than when it was large. The majority of our females laid spotted eggs (Table 2).

The Northern Masked Weaver (*P. taeniopterus*) nests in large colonies in eastern Africa and lays highly variable eggs. In a three-year study of this species in nature, Jackson (1990), studying at Lake Baringo, Kenya, observed that as many as a third of the nests contained an oddly-colored egg and, since cuckoo parasitism seemed to be rare there, she suggested that conspecific nest parasitism was more common in this species. In her egg-replacement experiments, rejection by a female of a "parasitic" egg was positively correlated with the degree of contrast in the background color of the host and parasitic egg.

Colonial nesting, so common in *Ploceus* weavers like the Village Weaver, might have promoted the evolution of egg variability as a counter defense against increased conspecific nest parasitism (Freeman 1988, Rohwer and Freeman 1989). Recently, Gowaty and Bridges (1991) used allozymic variation in blood proteins to confirm parentage in a population of Eastern Bluebirds (*Sialia sialis*) in the southeastern United States. They found that conspecific nest parasitism increased significantly in experimental areas where nesting pairs were relatively close together and abundant.

Another reason for high egg variability in the Village Weaver may be as a defense against obligate nest parasites, such as the Didric Cuckoo (*Chrysococcyx caprius*), the most common nest parasite of the Village Weaver (Chapin 1954, Friedmann 1968, Victoria 1969, 1972, Collias and Collias 1970, Collias 1984). This species of cuckoo may lay its eggs in the nest of the Village Weaver, as well as in the nests of over 50 other known species of birds, including 19 species of *Ploceus* weavers (Friedmann 1968:57).

In central Africa, Chapin (1954:355) referring to the Village Weaver noted that "The egg of the Didric may resemble eggs of the weaver very closely." However, in southern Africa the Didric Cuckoo's eggs may often also closely resemble eggs of two of its most commonly used fostering species, the Red Bishop (*Euplectes orix*; a weaver) and the Cape Sparrow (*Passer melanurus*; Payne 1967, Friedmann 1968:64). In western Africa, the nominate race of the Village

Weaver (*P. c. cucullatus*) is the most common host of the Didric Cuckoo (Fry et al. 1988). Like some eggs of the Village Weaver and of various other weaver species, the eggs of the Didric Cuckoo may be plain white or uniform greenish blue. They may also be white or pale green, with varying degrees of brownish and grayish markings (Friedmann 1968:74-75).

Female Village Weavers in Victoria's (1969, 1972) experiments in our aviaries were only one to a few generations removed from their ancestors in Senegal. Village Weavers of this same subspecies (*P. c. cucullatus*) were introduced from west Africa into Hispaniola in the Caribbean Sea as early as the 18th century. There were no brood parasites in Hispaniola until the early 1970s when Shiny Cowbirds (*Molothrus bonariensis*) arrived and began laying eggs in the nests of the Village Weavers which, as in the original homeland, nest in colonies. The cowbird's eggs are dissimilar to those of the weaver, but were accepted. In experimental egg replacements in Hispaniola, the Village Weaver was found to accept both dummy eggs and dissimilar eggs of the Village Weaver by Cruz and Wiley (1989), who suggested that relaxation of selection pressure for egg variability for about 200 years has resulted in the loss or decline of egg-rejection behavior by the Village Weaver in Hispaniola. Their observations would seem to favor interspecific rather than conspecific brood parasitism as the more important factor in the evolution of egg-color variability in the Village Weaver.

Parasitic species of birds and their fostering species have paced each other through evolutionary time with reciprocal adaptation and counter adaptation of egg mimicry by the parasitic species and egg variability by the foster species (Davies and Brooke 1989, 1991, Rothstein 1990). Interspecific and conspecific brood parasitism may both have been involved in the evolution of the high degree of egg-shell-color polymorphism seen today in some species of birds like the Village Weaver.

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