



POPULATION DIFFERENTIATION AND RAPID EVOLUTION OF EGG COLOR IN ACCORDANCE WITH SOLAR RADIATION

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ABSTRACT.—African populations of the Village Weaver (*Ploceus cucullatus*) are subject to brood parasitism by the egg-mimicking Diederik Cuckoo (*Chrysococcyx caprius*), which has resulted in high variation in egg color between individuals. Considering the nesting environment of the Village Weaver and the putative pre-parasitism ancestral egg color, I hypothesize that blue-green pigment may protect Village Weaver embryos from solar radiation. On this basis, more intense (more chromatic) blue-green egg colors may have evolved by natural selection in Village Weavers in the absence of Diederik Cuckoos. Moreover, even in African populations that are parasitized, Village Weaver eggs may have diverged in accordance with nesting light environments. In accordance with the proposed hypothesis, over the past two centuries two introduced populations have evolved more intense blue-green egg colors compared with their source populations. Two African source populations also differ from each other in the predicted direction, the population with the sunnier nesting climate having more intensely blue-green eggs. These results suggest that upon relaxation of brood parasitism by an egg mimic, Village Weaver eggs may adapt to solar radiation. Received 13 February 2007, accepted 23 February 2008.

Key words: bird eggs, egg color, introduced species, *Ploceus cucullatus*, rapid evolution, relaxed selection, solar radiation, Village Weaver.

Diferenciación entre Poblaciones y Evolución Rápida del Color de los Huevos de Acuerdo a la Radiación Solar

RESUMEN.—Las poblaciones africanas de *Ploceus cucullatus* están sujetas a parasitismo de cría por parte de la especie que imita huevos *Chrysococcyx caprius*, lo que ha conducido a una alta variación entre individuos en el color de los huevos. Considerando el ambiente de anidación de *P. cucullatus* y el color ancestral putativo previo al origen del parasitismo, planteé la hipótesis de que la pigmentación azul-verde podría proteger a los embriones de *P. cucullatus* de la radiación solar. Sobre esta base, los huevos de color azul-verde más intenso (más cromático) podrían haber evolucionado por selección natural en ausencia de *C. caprius*. Además, incluso en poblaciones africanas que son parasitadas, los huevos de *P. cucullatus* podrían haberse diferenciado de acuerdo a la luminosidad de los ambientes de anidación. De acuerdo a lo esperado según la hipótesis propuesta, a lo largo de los últimos dos siglos, los huevos de dos poblaciones introducidas han evolucionado hacia colores azul-verde más intensos en comparación con sus poblaciones originales. Dos poblaciones fuente ubicadas en África también difieren entre sí en la dirección predicha: la población con el clima de anidación más soleado presenta huevos con color azul-verde más intenso. Estos resultados sugieren que ante una disminución de la presión de parasitismo por parte de una especie imitadora de huevos, los huevos de *P. cucullatus* podrían adaptarse a la radiación solar.

BIRD EGG COLOR is a promising trait for evolutionary analysis because it appears to be subject to a modest array of selection pressures (Underwood and Sealy 2002, Kilner 2006) and because changes in egg color tend to be evolutionary (Punnett 1933, Gosler et al. 2000). “Ground color” is the relatively uniform background color of an egg, as opposed to spots or other markings that can also be present; in many cases, ground color and markings are subject to distinct sources of selection (Gosler et al. 2005, Westmoreland and Kiltie 2007). In the African Village Weaver (*Ploceus cucullatus*), both ground color and spotting of a female’s eggs are consistent

within a clutch and distinctive within the population. These traits permit a female to recognize her own eggs and thus avoid brood parasitism by the egg-mimicking Diederik Cuckoo (*Chrysococcyx caprius*, hereafter “cuckoo”; Victoria 1972, Lahti and Lahti 2002). Distinctiveness and consistency of egg colors have no known function besides egg recognition, and these traits decayed in 75–150 generations following two independent introductions to islands without egg-mimicking brood parasites (Lahti 2005). These changes, in turn, have compromised egg recognition in the introduced populations (Cruz and Wiley 1989, Lahti 2006).

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An unanswered question is what sources of selection remain to act on ground color of Village Weaver eggs when brood parasitism by cuckoos is removed as a factor. The ground color of Village Weaver eggs in Africa varies from white to medium greenish-blue (Collias 1984); in the introduced populations on the islands of Hispaniola and Mauritius, the egg colors are a subset of the respective ancestral ranges in western Africa and South Africa (Lahti 2005). Egg recognition may still function, to some extent, in the introduced populations in the context of conspecific parasitism (Freeman 1988), but there is no reason to believe that the extent of such parasitism would differ between source and introduced populations. Blue-green egg color does not appear to function in crypsis (Götmark 1992, Westmoreland and Kiltie 2007); regardless, crypsis would not aid Village Weaver eggs, because nests are enclosed and the eggs are not visible through the weave (Moreau 1960). A recently proposed signaling hypothesis (Moreno and Osorno 2003) relies on the inspection of eggs by males and subsequent modulation of paternal feeding behavior. This hypothesis is not relevant to the Village Weaver. Males do not generally have opportunities to observe egg colors, because males are excluded by females from the enclosed nests throughout the egg stage and have not been observed entering them; moreover, in none of the study populations do male Village Weavers regularly provision young (Collias and Collias 1971; D. C. Lahti pers. obs). One possibility is that egg ground color serves no function in the introduced populations. If so, ground color under relaxed selection might be expected to become more variable or—especially if there are costs to pigment production or deposition—to decrease in intensity.

An alternative hypothesis is that solar radiation has an influence on egg color that is detectable in the absence of functions for crypsis or egg recognition in this species. In particular, bird eggs may be subject to embryonic damage from solar radiation, and pigment may be photoprotective (McAldowie 1886, Romanoff and Romanoff 1949). Theoretically, solar damage to bird embryos can take two forms: conducted heat from light absorbed by the shell surface, and light transmitted through the eggshell. Pigment increases absorbance and so is unlikely to ameliorate conductance from the shell surface. Pigment decreases transmittance, however, and in so doing would decrease any adverse effects of light passing through the shell.

One possible detriment from transmitted light is embryonic heating. The optimal incubation temperature for bird eggs, usually 37–38°C, is close to the upper lethal limit for embryos (Webb 1987). Although bird eggs can sustain cold temperatures with little loss of viability, even a brief exposure to temperatures 2–3° higher than optimal results in a sharp decline in survival of embryos (Bartholomew and Dawson 1979, Bennett et al. 1981). Moreover, even moderate increases in embryonic temperature during the laying period (when eggs are maximally exposed) can initiate development and result in hatching asynchrony. Eggshells appear to be adapted to intercept solar heat via high infrared reflectance (Bakken et al. 1978). Eggshell color may modulate this effect, given that pigment blocks light from entering the eggshell (Romanoff and Romanoff 1949, Shafey et al. 2002), but whether the effect is great enough to be biologically significant is still uncertain (Kilner 2006, Westmoreland et al. 2007). There is likely a firm upper limit to how much pigment is beneficial in a given light environment, however, if the eggshell absorbs too

much solar radiation for the resulting heat to be dissipated, heat will build up in the shell and be conducted into the egg, ultimately killing the embryo. The only direct demonstrations of this possibility are with artificial pigments (Montevocchi 1976, Bertram and Burger 1981). Short of this extreme point, absorbance of light by eggshell pigment would be beneficial, insofar as it forestalls absorbance by the embryo.

Transmittance in the ultraviolet (UV) wavelength range can be a danger to vertebrate embryos irrespective of heating, causing developmental abnormalities even at common temperate levels of exposure (Blaustein and Belden 2003, Perotti and Diegeuz 2006). A poultry study (Shafey et al. 2002) showed that eggshells are particularly efficient at blocking UV light by absorbing it and that the brown eggs of at least one breed are more effective than white eggs in this regard. Biliverdin, the dominant pigment in blue-green eggs, has a high absorbance peak in the UV (Kennedy and Vevers 1973, Inomata et al. 2005). Consequently, biliverdin, including that occurring in eggs, has been hypothesized to function in photoprotection in invertebrates (McDonagh 2001), fish (Yamaguchi et al. 1976), and lizards (Austin and Jessing 1994).

In general, in moderate light environments where sunlight is filtered through vegetation, embryonic health and survival may be aided by blue-green eggshell pigmentation that can absorb and reflect incident solar radiation rather than allowing its transmission into the egg interior. In particular, because Village Weavers tend to nest in isolated trees and denude the vegetation around their nests (probably for predator-avoidance and mate-attraction functions; Collias and Collias 1959, 1969, 1970), their globular nests are commonly exposed to direct light throughout the day. The females generally lay eggs when the nests are still green (Jacobs et al. 1978); given the translucence of the nesting materials, the light environment of the nest's interior is blue-green, similar to a forest shade as described by Endler (1993). Blue-green eggs in such an environment would reflect light across the visible spectrum in proportion to the incident light intensity and would block UV transmittance as well. This hypothesis is consistent with the observation that the three ploceine weavers in Africa that build nests similar to that of the Village Weaver and appear not to have varying egg colors in response to brood parasitism—the Olive-headed Weaver (*P. olivaceiceps*), Cape Weaver (*P. capensis*), and Red-headed Weaver (*Anaplectes rubriceps*)—all lay unmarked blue-green eggs (Fig. 1).

The effect on fitness of too much versus too little density of pigment in an egg is expected to be asymmetrical. Transmittance of light through a too lightly colored eggshell can damage an embryo, but this damage is likely to be much less than that caused by conductance of heat into an egg through heat buildup in a too densely pigmented eggshell. Consistent with this idea, eggs in African Village Weavers vary from the medium blue-green of the eggs of the three rarely parasitized ploceine weavers almost only in having less, rather than more, pigment density. This circumstance suggests that selection by the cuckoo has influenced egg color variation in Village Weavers disproportionately in the direction of decreased rather than increased pigment. Thus, if Village Weaver egg color intensity, or chroma, is subject to selection by solar radiation, the mean chroma of African Village Weaver eggs is probably below the solar optimum. Two predictions follow. First, egg variability for avoidance of brood parasitism ensures that

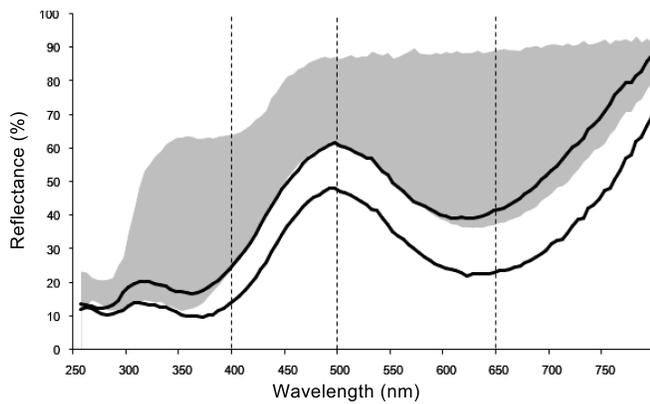


FIG. 1. The range of reflectance spectra of eggs of the African Village Weaver (shaded area), and typical eggs from the Red-headed Weaver (upper black line) and Cape Weaver (lower black line). Dotted lines indicate points at which measurements were taken to represent egg chroma. The upper bound to the Village Weaver egg area is the reflectance of a white egg, and the lower bound is that of a medium blue-green egg. The Red-headed and Cape weaver eggs are similar in chroma to the most chromatic Village Weaver eggs (though the Cape Weaver egg is darker) and represent a plausible ancestral egg chroma of Village Weavers before parasitism by cuckoos (see text).

there is genetic variance for eggshell chroma. Therefore, in addition to frequency-dependent selection by the cuckoo, selection by solar radiation may produce a detectable response in Africa. In particular, higher intensity of solar radiation at the nest should translate into more selection for increased chroma (toward the putative ancestral solar optimum); so sunnier populations should lay more intensely blue-green eggs, on average. Second, eggs in the introduced (unparasitized) Village Weaver populations should have more blue-green chroma than eggs in the respective source (parasitized) populations, because the introduced populations are free to evolve toward the solar optimum from which selection by the cuckoo had displaced them. Here, I provide a provisional test of the hypothesis of adaptation of egg color to solar radiation, by comparing mean egg chroma across Village Weaver populations in light of these predictions.

METHODS

I collected Village Weaver clutches three days or fewer after clutch completion from four localities: Janjangbureh Island, The Gambia, western Africa (13°35'N, 14°40'–50'W; July–August 1999; $n = 130$); Pietermaritzburg, KwaZulu-Natal, South Africa (29°25'–45'S, 30°25'–35'E; October–December 2000; $n = 69$); Black River and Rivière du Rempart Divisions, Mauritius (20°00'–20'S, 57°20'–40'E; December 2000 to February 2001; $n = 69$); and Monte Cristi and Valverde Provinces, Dominican Republic, Hispaniola (19°35'–45'N, 71°00'–20'W; April–June 2001; $n = 130$). The Gambian population was the source of an introduction of Village Weavers to Hispaniola before 1800, and the South African population was the source of an introduction to Mauritius in 1886 (Lahti 2003).

Blue-green chroma was characterized for one egg chosen at random from each available clutch in the two introduced populations (Mauritius and Hispaniola) and their respective source populations (South Africa and The Gambia) by subtracting reflectance at 500 nm from the mean of the reflectances at 400 nm and 650 nm, thereby capturing the size of the reflectance peak that characterizes blue-greenness (Fig. 1). Reflectances were obtained in the laboratory, from blown eggs collected in the field, with an Ocean Optics USB2000 UV-VIS spectrophotometer and OOIBase32 software (Ocean Optics, Dunedin, Florida). I assessed reflectance at 5-nm intervals over the wavelength range of 250–800 nm with a 200-Hz pulsed xenon light source (Ocean Optics PX-2), and a 400- μ m 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 polytetrafluoroethylene that reflects >98% of light over all sampled wavelengths (Ocean Optics WS-1). I performed all measurements under an opaque cloth to avoid an effect of ambient light. One measurement was taken per egg, approximately halfway between the poles, in an area that appeared, under a dissection scope, to be representative in color and unspotted.

To address the prediction that eggs are more chromatic in populations with stronger sunlight, light environment should be assessed during laying, when eggshells are most translucent and bird nests are most often left unattended. I performed these studies in months that are considered peaks of Village Weaver breeding intensity in the respective study areas (Morel and Morel 1959, Clancey 1964, Maclean 1993). I observed females laying their initial eggs during cloud cover or rain in South Africa more frequently than in The Gambia or in the two introduced island populations, where nests were usually in full sun all day (Table 1). Weather stations near both African study sites have historically registered similar mean numbers of rain days (~15) for the peak months of Village Weaver breeding (World Weather Information Service, World Meteorological Organization). Cloud cover and rain in The Gambia are ephemeral, usually occurring briefly in the afternoon, such that Village Weaver nests were in full sun for most of every day of observation. The South African study site, however, experiences frequent and consecutive overcast days, so nests there are regularly in a condition of low light intensity. These observations are corroborated by World Radiation Data Centre records of sunshine and solar radiation within 100 km of each study area during the main months of Village Weaver breeding, roughly the summer half of the year in both study areas: September–February in KwaZulu-Natal (Clancey 1964, Dean 1971) and April–September in The Gambia (Morel and Morel 1959, D. C. Lahti pers. obs.). World Radiation Data Centre data were available from Durban, South Africa, between 1969 and 1974 for sunshine and between 1964 and 1974 for solar radiation, and from Bassé, The Gambia, for 1980 only. The vicinity of the study area in The Gambia received a mean of 238.8 h of sunshine per month between April and August. This is far higher than any record for KwaZulu-Natal, whose mean monthly sunshine for September–February was 177.9 h (SD across years: 9.5). Likewise, mean daily solar radiation at ground level during the Village Weaver breeding season was 2,174 J cm⁻² from April to August near the Gambian study site, but only 1,848 J cm⁻² near the South African study site. Day-to-day variation in solar radiation in a

TABLE 1. Incidence of cloud cover during the first day of egg laying in the Village Weaver, across populations.

Population	Location	Dates	Egg laying under cloud cover ^a
South Africa	Near Pietermaritzburg, KwaZulu-Natal, 29°25–45°S, 30°25–35°E	October–December 2000	70 of 115 nests (61%)
The Gambia	Janjangbureh Island, 13°35'N, 14°40–50'W	July–August 1999	13 of 57 nests (23%)
Mauritius	Black River and Rivière du Rempart Divisions, 20°00–20°S, 57°20–40°E	December 2000–February 2001	0 of 56 nests
Hispaniola	Monte Cristi and Valverde Provinces, 19°35–45°N, 71°00–20°W	April–June 2001	10 of 149 nests (7%)

^aThe comparison between South Africa and The Gambia (chi-square test) is significant at $P < 0.00001$.

month was also much higher in South Africa, the standard deviation of solar radiation across days in a month being, on average, 713, as compared with 363 in The Gambia.

Egg chroma estimates for each population were compared in paired t -tests using SYSTAT, version 10.0 (SPSS, Chicago, Illinois).

RESULTS

Mean blue-green chroma of Village Weaver eggs was higher in The Gambia than in South Africa ($G/SA t_{68} = 3.50, P = 0.0008, m_{G-SA} = 4.3\%$; Fig. 2). Village Weaver eggs increased in blue-green chroma

following introduction from South Africa to Mauritius ($SA/M t_{68} = 3.15, P = 0.002, m_{M-SA} = 3.8\%$; Fig. 2). Likewise, Hispaniolan eggs converged on a narrow range of blue-green whose mean is higher in chroma than that of the Gambian population ($G/H t_{129} = -6.37, P < 0.0000001, m_{H-G} = 4.4\%$; Fig. 2). An obvious difference between the eggs in The Gambia and those on Hispaniola is the lack of white and off-white eggs in the latter population (Lahti 2005). It is possible (though unlikely, given that Village Weavers were introduced in several events) that such eggs are absent from Hispaniola because of biased characteristics of the introduced individuals (founder effect). When eggs of these colors ($n = 28$) are removed from the Gambian data set, the higher chroma on Hispaniola remains significant ($P = 0.003$).

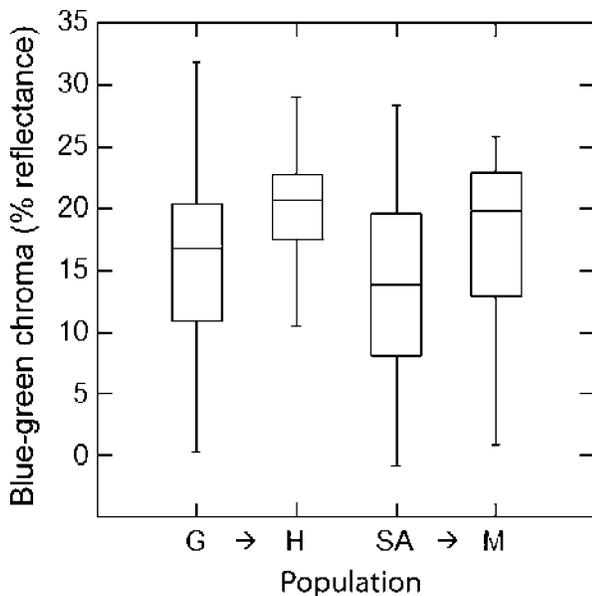


FIG. 2. Intensity of blue-green chroma in Village Weaver eggs across populations, showing an increase in chroma following introductions and higher chroma in the African population with the more intense light environment. Arrows indicate introductions of species. G = The Gambia, H = Hispaniola, SA = South Africa, M = Mauritius. Blue-green chroma is the difference between eggshell reflectance at 500 nm and the mean of the reflectances at 400 nm and 650 nm. Horizontal lines are median values, boxes encompass ± 1 SD from the mean, and whiskers encompass the values from all sampled eggs.

DISCUSSION

During the past two centuries, two independently introduced tropical island populations of the Village Weaver have evolved more intense blue-green egg colors compared with their source populations. This change is consistent with the hypothesized effect of solar radiation in the absence of selection pressure from cuckoos. The two African source populations also differ from each other in the predicted direction, the population with the sunnier nesting climate having more intensely blue-green eggs.

These changes, as with the previously documented changes in egg color variation observed in these populations, are likely evolutionary (Lahti 2005, 2006). A long-term study of captive Village Weavers has shown that a female tends to lay eggs with a consistent ground color throughout her life (Collias 1984, 1993). In wild populations, however, differences in egg ground color may reflect female condition (Siefferman et al. 2006), egg color may change as a function of stress or pollutants (Arendt 2004, Jagannath et al. 2008), and pigment production or deposition may bear a cost (Moreno and Osorno 2003). Nevertheless, the egg color differences observed in the present study were population-wide and characterized by a decrease in variation compared with the ancestral populations, in proportion to the time since introduction (Lahti 2005). This situation is more consistent with evolutionary change in response to selection than with plastic individual responses to environmental conditions. Village Weavers are populous agricultural pests in all four study populations (Lahti 2003) and bred continuously and with frequent success throughout the

period of sampling. There was no indication of a widespread difference in condition across populations, though this was not directly tested. Even if condition varied between populations, this would still leave open the question of what function blue-green egg pigment serves in this species, apart from avoiding cuckoo brood parasitism. The present observations taken together are most consistent with the hypothesis that Village Weaver egg color diverged between populations by natural selection for protection from solar radiation.

Placed into a broader evolutionary context with other available evidence, these results suggest the following chain of events. The ground color of the ancestral ploceine weaver egg, before the onset of cuckoo brood parasitism, was medium blue-green (Fig. 1), as in many birds that nest in light filtered through vegetation (Lack 1958). In the course of an "arms race" with a brood-parasitic cuckoo, egg mimicry evolved in the cuckoo and variation in egg ground color and spotting evolved in the Village Weaver, among other traits. But the ground color of Village Weaver eggs did not become variable in both directions equally; rather, evolutionary decreases in pigment density were much more common than increases from the ancestral condition, perhaps because an increase in pigment density beyond the optimal level would decrease egg viability through overheating. Thus, Village Weavers in Africa today lay eggs that range from white to medium blue-green, so the mean observed chroma level is likely below the solar optimum. Nevertheless, despite the swamping effect of frequency-dependent selection by the cuckoo, differences in intensity of solar radiation in different populations still affect egg colors. Mean egg color is more intensely blue-green in sunnier western Africa than on the more temperate and cloudy east coast of South Africa. Moreover, following independent introductions of the Village Weaver to two islands devoid of egg-mimicking brood parasites, Village Weaver eggs were no longer constrained by selection pressure from cuckoos and evolved higher (more protective) chroma in response to selection by solar radiation.

These interpretations must be viewed as preliminary, for two reasons. First, the environmental measurements were coarse and the sample of populations small. A more precise test within Africa, for instance, would include irradiance spectra from inside Village Weaver nests and typical solar radiation intensity for each habitat. Nevertheless, the difference in solar radiation between the two African study sites is great enough that more quantitative measurements would not affect the general prediction. However, a more extensive coverage of African Village Weaver eggs, or of other species with broad geographic ranges, would test the generality of the present study's finding. Second, the predictions tested here could be refined for a more powerful test of the influence of solar radiation on Village Weaver egg evolution. Such refinement is impossible at this time, because no quantitative data are available that relate egg color to egg heating and light transmittance, despite the interest in egg color and incubation efficiency in poultry research (e.g., Lang and Wells 1987, Wei and Bitgood 1990, Kirikci et al. 2005). Consequently, the relationship between egg color and survival of embryos has not yet been modeled. Such developments would facilitate more specific predictions as to the optimal degree of blue-green chroma in a given light environment.

The changes in eggshell chroma described here represent population differentiation and rapid evolution in line with qualitative predictions from the expected effect of solar radiation on egg viability. Therefore, this situation may provide an example of adaptation to one source of selection following the relaxation of another, previously stronger, source of selection. Moreover, the particular system in which these observations were made raises the possibility that a solar-radiation hypothesis may help answer the long-perplexing question of why many birds lay blue-green eggs.

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