

# Evolution of bird eggs in the absence of cuckoo parasitism

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**Historical introductions of species into new habitats can create rare opportunities to test evolutionary hypotheses, such as the role of natural selection in maintaining traits. This study examines two independent introductions of the African village weaverbird (*Ploceus cucullatus*) to islands where selection on egg appearance traits is expected to differ markedly from that of the source populations. The color and spotting of village weaver eggs in Africa are highly consistent within clutches, but highly variable between individuals. These two features may be an evolutionary response to brood parasitism. In Africa, weavers are parasitized by each other and by the diederik cuckoo (*Chrysococcyx caprius*), an egg mimic. African village weavers were introduced one century ago to Mauritius, and over two centuries ago to Hispaniola. Both islands are devoid of egg-mimicking brood parasites. In these two populations, between-individual variation and within-clutch consistency in egg appearance have both decreased, as has the incidence of spotting, relative to the source populations in Africa. These reductions are more pronounced on Hispaniola, the earlier introduction. Such changes support the hypothesis that egg appearance in the African village weaver has been maintained by natural selection as a counteradaptation to cuckoo brood parasitism. These results illustrate that the removal of an agent of selection can sometimes bring about rapid evolutionary consequences.**

brood parasitism | introduced species | Ploceidae | rapid evolution | trait loss

Species introductions can reveal the operation of natural selection as a mechanism of evolution when environments of source and introduced populations differ in ways that lead to evolutionary predictions (1–3). Evolution in introduced populations can be rapid, even in vertebrates (4), and researchers can use the source population as a control for changes observed in the introduced population (5). This study takes advantage of environmental differences between two source and two introduced populations of the African village weaverbird (*Ploceus cucullatus*) to test for the role of natural selection in maintaining variation in egg appearance.

Avian brood parasites lay eggs in the nests of other birds. In Africa, the village weaver is a regular host of the diederik cuckoo (*Chrysococcyx caprius*). The diederik is an obligate brood parasite that has evolved to lay eggs that mimic weaver eggs in appearance. Diederik chicks generally hatch early and remove any other eggs or young from the nest, nullifying the weaver's reproductive attempt (6, 7). Village weavers may also be brood parasites of each other, as indicated by the discovery of mismatched weaver eggs in nests, and more extensive observations in closely related species (8–10). Conspecific brood parasitism is most often observed in species where nests are conspicuous and clustered, as in the village weaver (11). When successfully parasitized by either a cuckoo or a conspecific, a weaver incubates the egg and raises the hatchling to independence.

As a defense against brood parasitism, village weaver females learn the appearance of their own eggs and expel foreign eggs from their nests (12), thereby avoiding much of the cost of parasitism (13). In a test of this egg rejection behavior, Lahti and Lahti (14) switched conspecific eggs among nests of village

weavers in West Africa, and observed their responses. Birds rejected eggs in proportion to differences in color and spotting pattern between the foreign eggs and their own.

To maximize effectiveness of egg rejection behavior as a defense against brood parasitism, a village weaver's eggs should possess two features. First, they should be distinctive within the population; weaver eggs should have high between-individual variation, as indeed they do in Africa (9, 15). Although no quantitative comparative study has yet been performed, the level of population variability in egg appearance found in African *Ploceus* weavers is extreme among birds. The more unusual a weaver egg is in its population, the more likely a parasitic egg laid in its nest will differ from it sufficiently for the host to detect and remove it; whereas a weaver egg of common appearance will be more likely to be matched. This dynamic is expected to maintain a diversity of egg appearance across a village weaver population. Second, a weaver's eggs should be consistent with each other, or have low within-clutch variation (16). High uniformity of eggs within a host clutch minimizes the window of opportunity for the brood parasite: it decreases the number of individuals that could successfully parasitize the host.

Per incidence, cuckoos exert stronger selection for host defenses than conspecifics (17). First, conspecific brood parasitism does not usually ruin the reproductive attempt of the host, because parasitic young usually develop alongside host young. Second, conspecific parasites are also susceptible to parasitism themselves, so individual costs and benefits of parasitism may cancel each other out to some extent. Diederik cuckoos, on the other hand, are expected to coevolve with weavers in egg appearance, maximizing their own reproductive success by matching common weaver eggs, and in turn exerting frequency-dependent selection on weaver egg appearance (18). Likewise, natural selection for egg recognition by hosts is expected to be intense where cuckoo parasitism is a consistent threat (19). Nevertheless, cuckoo (12, 20–22) and conspecific (9, 10) parasitism could both be important agents of selection on village weaver egg appearance and egg rejection behavior in Africa.

The village weaver was introduced from West Africa to the Caribbean island of Hispaniola during the colonial period from before the 1790s (23). A small number of individuals were also introduced from Southern Africa to the island of Mauritius in a single event in 1886 (23). No reports exist of later introductions into either population. On both islands, the weavers are now abundant and presumably experience no gene flow with other populations. Although the diederik cuckoo is a threat to the village weaver throughout the weaver's range in Africa, neither the diederik cuckoo nor any other egg-mimicking brood parasite exists in the two introduced ranges. The only potential interspecific brood parasite of the weaver in either introduced range is the shiny cowbird *Molothrus bonariensis*, which reached Hispani-

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ola in the 1980s, and whose eggs do not resemble those of Hispaniolan weavers (20).

In this study, I examine these two introduced populations and their source populations to test the hypothesis that variation in egg appearance and uniformity within a clutch have been maintained by natural selection as counteradaptations to cuckoo parasitism. In Africa, where egg-mimicking cuckoo parasitism occurs and perhaps conspecific parasitism, egg color and spotting are used in egg recognition (14). I predicted that, if cuckoo parasitism is an important agent of selection, then after introduction to habitats without cuckoos, variation in weaver egg color and spotting should decrease between individuals and increase within a clutch. Although no direct tests have been performed, there is no reason to suppose that conspecific parasitism is high in Africa and declined precipitously in both introduced populations. Colony sizes and percentages of active nests per colony were similar across all four study sites. On the assumption of similar levels of conspecific parasitism in the source and introduced populations, I predicted no particular changes in egg appearance if conspecific parasitism is an important agent of selection.

## Methods

**Egg Collection.** I collected village weaver clutches 3 days or fewer after clutch completion from the following localities: Janjangbureh Island, The Gambia, West Africa (13°35' N, 14°40'–50' W; July to August 1999;  $n = 107$ ); Pietermaritzburg, KwaZulu-Natal, South Africa (29°25'–45' S, 30°25'–35' E; October to December 2000;  $n = 122$ ); Black River and Rivière du Rempart Divisions, Mauritius (20°00'–20°S, 57°20'–40' E; December 2000 to February 2001;  $n = 52$ ); and Monte Cristi and Valverde Provinces, Dominican Republic, Hispaniola (19°35'–45' N, 71°00'–20' W; April to June 2001;  $n = 154$ ). Hereafter,  $G_s$  and  $SA_s$  indicate source populations from The Gambia and South Africa, respectively, and  $M_i$  and  $H_i$  indicate introduced populations from Mauritius and Hispaniola, respectively.

Clutches varied between one and four eggs. One-egg clutches were excluded from within-clutch variation analyses. To prevent site differences in average clutch size from biasing analyses of egg appearance variability, analyses were based on two random eggs (an “effective clutch”) from clutches of more than two eggs.

**Measurements.** The main methodological objective was to quantify between-female variability and within-clutch uniformity in the four populations. Measurements of egg appearance focused on shape, mass, ground color, and spotting. For each egg characteristic, all measurements across all study sites were performed by a single person. Shells of eggs used in analyses are deposited in the University of Michigan Museum of Zoology.

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

I matched eggs to color chips in the *Villalobos Color Atlas* (24) as described (14). I also brought eggshells back to the U.S. and measured eggshell reflectance in the laboratory with an Ocean Optics USB2000 UV-VIS spectrophotometer and OOIBASE32 software (Ocean Optics, 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- $\mu$  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. 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. Reflectance data were reduced by principal components analysis.

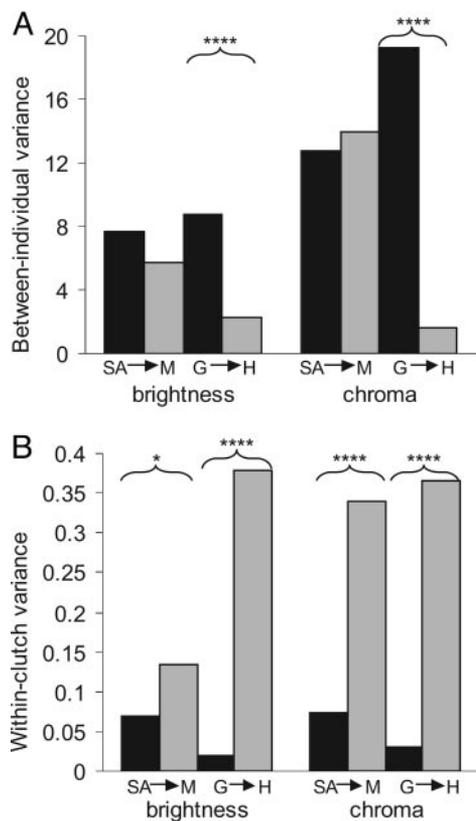
I assessed four aspects of eggshell spotting: size, density, and color of spots, and the degree of aggregation at the cap (broad end) of the egg. I ranked each spotted egg in the field into one of three categories for each variable. I later confirmed the consistency of the categorization by obtaining quantitative measurements. For spot size, density, and cap aggregation, 16 representative eggs were measured per level, four from each population. For spot color, reflectance spectra of spots were obtained for five representative eggs per level. In all cases, eggs from different qualitative categories had nonoverlapping quantitative measurements.

**Statistical Analysis.** Data analysis was performed by using SYSTAT (version 10.0, SPSS, Chicago). For continuous variables (relating to egg shape, mass, and color), I compared variation in egg appearance using a variance method and a disparity method. First, I calculated within-clutch and between-individual variances for each population from ANOVA sums of squares. I compared these between source and introduced populations with two-tailed  $F$  tests, Bonferroni-adjusted for multiple comparisons. Second, I calculated within-clutch disparity, the difference in value between the two eggs in each effective clutch in a population. I assessed between-individual disparity by calculating the difference between an egg in each clutch and an egg from another clutch in the population, selected at random. I used ANOVA to compare the population means of these disparity values and used the Bonferroni adjustment to obtain significance values for pairwise comparisons. The two methods produced similar results except where noted.

Only the disparity method was appropriate for calculating variation in categorical (egg spotting) variables. I compared population means for within-clutch and between-individual disparity with the Kruskal–Wallis/Mann–Whitney  $U$  test. Levels of significance in the Mann–Whitney  $U$  test can be distorted when there are too many tied values, which are common in the spotting variables. Therefore, I also recoded spotting disparity within clutches as binary (difference/no difference) and compared populations by a  $\chi^2$  test for independence. No qualitative differences were found between the two methods, so only Mann–Whitney  $U$  results are presented here.

## Results

**Between-Individual Variation.** Principal component analysis reduced the variation in the spectral (color) data to three components. The first factor corresponded closely to spectral brightness, and the second and third factors represented aspects of chromatic variation (as in ref. 25). As predicted, the introduced weaver population on Hispaniola had a lower level of variation between individuals than did the Gambian population in egg color and spotting. Significant differences were found for brightness (color chart variance:  $F_{111,143} = 3.83$ , Fig. 1A; color chart disparity: ANOVA,  $F_{3,499} = 12.1$ , Fig. 2A; spectral variance: PC1,  $F_{105,153} = 5.81$ ,  $P < 0.00001$ ; spectral disparity: ANOVA,  $F_{3,433} = 18.5$ , Fig. 2B), chroma (color chart variance:  $F_{111,143} = 11.8$ , Fig. 1A; color chart disparity: ANOVA,  $F_{3,499} = 35.0$ , Fig. 2C; spectral variance: PC3,  $F_{105,153} = 4.51$ ,  $P < 0.00001$ ; spectral disparity: PC2,  $F_{3,431} = 7.5$ , Fig. 2D), and spot color (Mann–Whitney  $U = 8,575$ , Fig. 3A). The introduced population on Mauritius also showed reduced between-clutch variation in comparison to the South African population, but the magnitude of these differences were smaller and most were nonsignificant. A significant difference was found in chroma (spectral variance: PC3,  $F_{106,51} = 3.26$ ,  $P = 0.00003$ ), and there were trends in brightness (spectral disparity: PC1, ANOVA,  $F_{3,433} = 18.5$ , Fig. 2B), chroma (spectral variance: PC2,  $F_{106,51} = 3.26$ ), and spot size ( $U = 3,742$ , Fig. 3A).

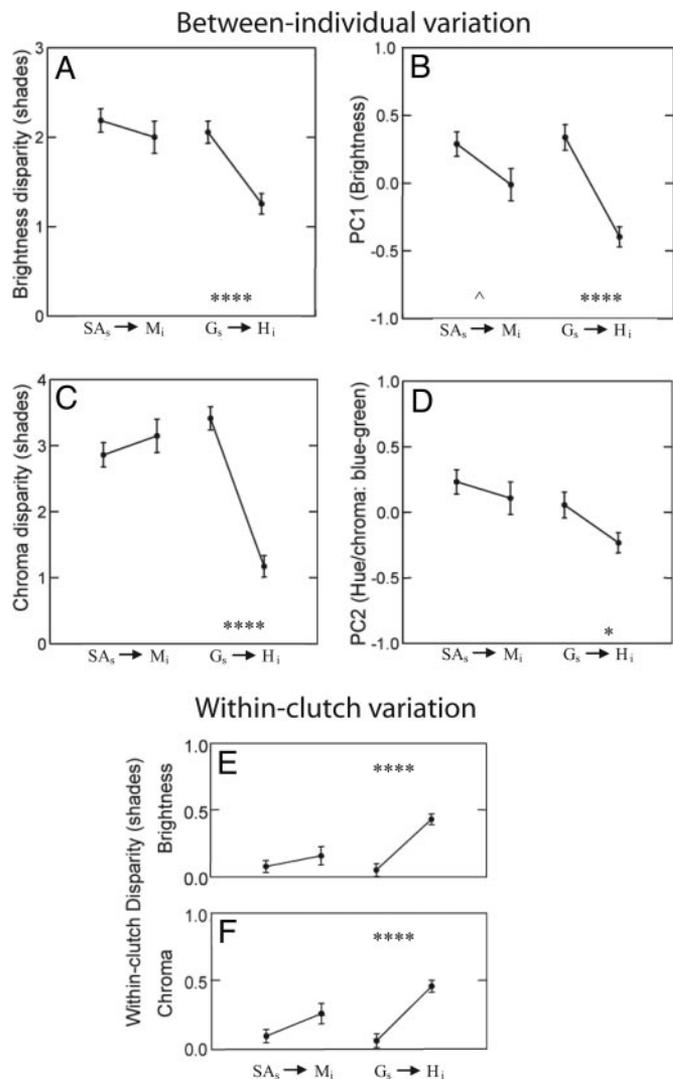


**Fig. 1.** Variance in egg color across village weaver populations, calculated from ANOVA sums of squares, based on color charts. SA, South Africa; M, Mauritius; G, The Gambia; H, Hispaniola. Arrows indicate introductions of the species. Significance levels after adjustment to a two-tailed  $F$  test and Bonferroni correction: \*,  $P < 0.05$ ; \*\*\*\*,  $P < 0.00001$ .

**Within-Clutch Variation.** Repeatability of reflectance measurements was low enough (SD of 10 measurements of the same egg was 5.6) to swamp typical within-clutch differences in egg color (mean SD of a clutch in The Gambia = 3.6). Therefore, only color chart data were included in within-clutch analyses. In accordance with predictions, clutches were more variable in the introduced populations than they were in the respective source populations in most measures of egg color and spotting. Significant differences were found in all measures of color and spotting between The Gambia and Hispaniola (brightness disparity: ANOVA,  $F_{3,431} = 16.8$ , Fig. 2E; brightness variance:  $F_{143,111} = 19.9$ , Fig. 1B; chroma disparity: ANOVA,  $F_{3,431} = 15.8$ , Fig. 2F; chroma variance:  $F_{143,111} = 11.8$ , Fig. 1B; spot size:  $U = 9,514$ ; spot density:  $U = 9,665$ ; spot color:  $U = 8,681$ ; spot aggregation:  $U = 9,657$ , Fig. 3B). Weavers on Mauritius had less consistent clutches than in South Africa, as predicted, although the differences were again smaller and fewer were significant. Significant differences were found for brightness (variance:  $F_{51,121} = 1.93$ , Fig. 1B), chroma (variance:  $F_{51,121} = 4.59$ , Fig. 1B), and spot color ( $U = 3,624$ , Fig. 3B); and two other spotting variables exhibited trends (spot density:  $U = 3,499$ ; spot aggregation:  $U = 3,532$ , Fig. 3B).

**Other Measurements.** The two African (source) populations did not differ significantly in most egg appearance traits, and directions of differences were not concordant across traits.

Variation in egg shape and mass between individuals did not differ statistically across populations. Within clutches, egg shape did not vary across populations, although variance in egg mass



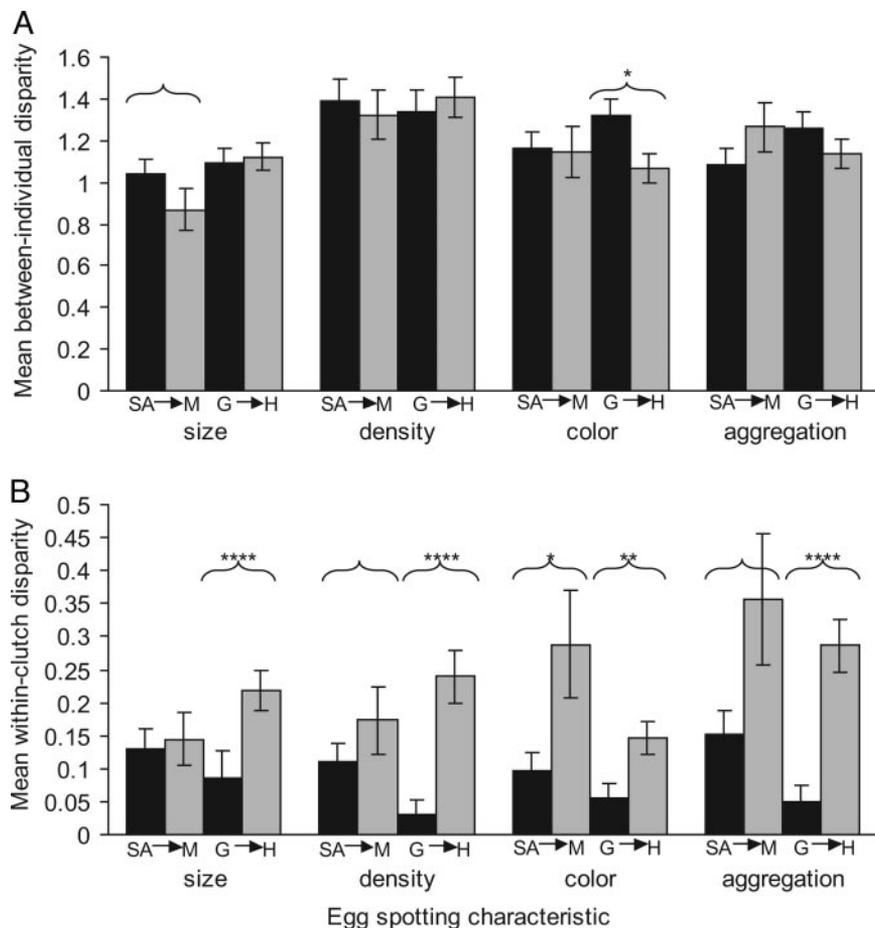
**Fig. 2.** Mean disparity in egg color across village weaver populations, based on color charts (left) and spectral analysis (right). Bars indicate SE. Significance levels after Bonferroni correction: ^,  $P < 0.1$ ; \*,  $P < 0.05$ ; \*\*\*\*,  $P < 0.00001$ .

was lower in clutches from The Gambia than in those from Hispaniola ( $F_{133,58} = 2.08$ ;  $P < 0.01$ ).

In analyses of eggs from The Gambia and Hispaniola, I noted instances when an egg appeared inconsistent in color over its surface because of mottling, unpigmented spots, or a darker band in one area of the egg. I identified 16 of 177 eggs (9%) in The Gambia, as compared to 59 of 271 eggs (22%) in Hispaniola ( $\chi^2$ :  $P = 0.0004$ ) with such inconsistency. This finding affected 14 of 125 clutches (11%) in The Gambia and 33 of 164 clutches (20%) in Hispaniola ( $\chi^2$ :  $P = 0.042$ ).

The proportion of individuals 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 Hispaniola than in The Gambia ( $\chi^2$ :  $P = 0.025$ ).

**%BI as an Index.** The percentage of total variation in an egg appearance characteristic that is between-individual rather than within-clutch (%BI) reflects the effectiveness of that characteristic for egg recognition. In both African (source) populations, almost all (99.1–99.8%) of the variation in egg color (brightness and chroma) was between individuals. For all color and spotting



**Fig. 3.** Mean disparity in egg spotting characteristics across village weaver populations: size, density, color, and aggregation of spots near the cap (broad) end of the egg. Bars indicate SE. Significance levels after Bonferroni correction: bracket alone,  $P < 0.1$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*\*,  $P < 0.00001$ .

variables, %BI was lower in each introduced population than in its source population. On Hispaniola, %BI was 14–27% lower than in The Gambia for color variables, and 8–16% lower for spotting variables. On Mauritius, %BI was 1–4% lower than in South Africa for color variables, and 3–12% lower for spotting variables.

### Discussion

The results support the hypothesis that egg appearance in the African village weaver is maintained by natural selection as a counteradaptation to cuckoo brood parasitism. African populations of the village weaver suffer brood parasitism by the diederik cuckoo and perhaps conspecifics. They lay eggs that vary greatly between individuals but are uniform within a clutch. These features of distinctiveness and consistency in egg appearance permit a female to recognize and eject a foreign egg more readily. In two introduced populations, village weavers are free from cuckoo parasitism, but presumably retain levels of conspecific parasitism similar to their source populations in Africa. In the introduced populations, features of egg appearance that are used in egg recognition are less variable between individuals, and more variable within a clutch, compared to their source populations. Moreover, the incidence of spotting on eggs is also lower in the introduced populations.

**Egg Appearance Evolution.** Village weavers that were introduced to Mauritius have lost some percentage of the reliability for egg recognition of each egg color and spotting variable. Between-individual variance decreased in spectral chroma, with trends

( $P < 0.1$  after Bonferroni correction) toward increases in brightness and spot size disparity; and within-clutch variation decreased in brightness, chroma, and spot color, with trends toward a decrease in spot density and cap aggregation. The remaining differences in within-clutch and between-individual variation between Mauritius and South Africa, although non-significant, were in the predicted direction for all measures of egg color and spotting; the one exception was egg chroma as determined from color charts, its slight change inconsistent with spectral data. As a whole, results from the Mauritian population point to 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 Hispaniola, where weavers likewise do not experience the cuckoo parasitism that occurs in West Africa. Between individuals, egg color variation decreased in both brightness and chroma, whether assessed by color charts or spectrophotometry. These differences were readily apparent to a human observer. No white or light-colored eggs were present in Hispaniola, whereas they were common in the other three populations. Variation in spot color also decreased between individuals; changes in the other three spotting variables were not significant, but were in the predicted direction. Within a clutch, variation increased significantly and strongly in all color (brightness and chroma) and spotting variables (size, density, color, and cap aggregation). These changes were obvious to an observer. Unlike in The Gambia, the amount of pigment deposited as ground color in Hispaniola often varied conspicuously within a clutch, and varied twice as often even within an



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hermaphrodite reproductive tract. Nonspecific protease cleavage may not be sufficient, as Pronase treatment can activate sperm but these sperm lose their ability to fertilize eggs [19]. Perhaps the hermaphrodite reproductive tract is not a great source of specific activating proteases but is good enough to support wild-type fertility. The effects of crippling some aspects of the activation pathway — as in the *spe-8* group mutants — reveal a differential sensitivity to available proteases in hermaphrodites versus males. Sorting out the real differences between male and hermaphrodite sperm activation and fully defining the nature of the components of the spermiogenesis pathway(s) — for example, identifying key proteases and new sperm components — are clearly important tasks. Follow up studies on *swm-1* and the analysis of other mutants isolated in Stanfield and Villeneuve's [14] genetic screen promise exciting new insights into factors critical for reproductive success.

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## Evolution: Mothers 'Sign' Their Eggs Where Cuckoos Lurk

A new study has demonstrated that African village weaver birds (*Ploceus cucullatus*) show less individuality in the appearance of their eggs when freed from the threat of raising the young of egg-mimicking diederik cuckoos (*Chrysococcyx caprius*). This suggests another clear example of natural selection driving evolutionary change *in situ*.

Sasha R.X. Dall

Evidence for evolution by natural selection has been at a premium in the biological sciences. Even now, with neo-Darwinism firmly ensconced as the central pillar of modern biology, a convincing example of natural selection generating evolutionary change always catches the eye. Indeed, in today's climate of ideologically motivated attacks on the

teaching of modern evolutionary biology in certain parts of the world, science educators can always use uncontroversial, easy to explain case studies of 'evolution in action'. A recent study by Lahti [1] may provide such an example by documenting apparent changes in egg appearance in African village weaver bird (*Ploceus cucullatus*; Figure 1) populations liberated from an ancestral brood parasite:

the diederik cuckoo (*Chrysococcyx caprius*).

It is intuitively appealing to conceive of natural selection as requiring changes in the physical environment of a population. Symptomatic of this is the iconic status of industrial melanism in the peppered moth, *Biston betularia*. The rise of the black, *carbonaria* form of the moth in response to changes in the environment caused by the industrial revolution in Britain is probably the best known, if somewhat controversial, example of evolution in action. In the mid-1800s, entomologists recorded the appearance of *carbonaria* peppered moths around Manchester, and by the end of the 19th century 98% of that population was black. The *carbonaria* form spread to many

other parts of Britain, reaching high frequencies in industrial centers and neighboring regions.

It was surmised that this increase in prevalence resulted from differential predation of the ancestral speckled (*typica*) form of the moth by birds while individuals rested against the soot-stained bark of polluted trees [2]. Such a view is corroborated by the observation that, since the enforcement of British anti-pollution legislation in the 1950s, the *carbonaria* frequency has declined dramatically [2], and a similar story has been documented in the United States [3]. Furthermore, in the 1950s, Kettlewell [4,5] famously showed that speckled moths suffered higher rates of predation when released into polluted woods, while the melanised morph suffered heightened predation in unpolluted woods. Although this definitive line of evidence is proving somewhat controversial at the moment [6], the appeal of this case study to all sides of the evolutionary debate reflects how easy it is to understand and communicate. Nevertheless, evolution by natural selection is also possible in the absence of changes to the physical environment of a population.

To evolve by natural selection, biological variants must replicate differentially. Where the raw materials for life are limited, this generates pools of reproductive lineages that are in perpetual competition with each other for access to resources. As a result, other interacting lineages constitute a major component of the environment to which individual lineages will adapt. Hence, it is possible for evolutionary change to occur in the absence of physical changes to the environment. Furthermore, physical changes to the environment often generate selection by altering such biotic interactions — in the case of industrial melanism, it is likely that fluctuating pollution levels only selected for heritable changes in peppered moth coloration by changing the predation efficacy of local birds [7].



Figure 1. An African village weaver bird at a partially constructed nest.  
From: <http://www.pyasafari.co.uk/fotogalerie/vogels.php> (photo: Jan van Duinen).

Interactive evolutionary dynamics between multicellular organisms and their microbial pathogens are thought to be a major factor underlying the predominance of sexual reproduction in metazoans [8]. As microbial parasites can go through thousands of generations for every one of their metazoan hosts, relying on conventional ‘mutation-driven’ evolution alone would allow the parasites to adapt easily to host defences. To stay ahead of the game then, one host tactic is to differentiate offspring each generation, both from parents and from the progeny of others, to keep defensive ‘targets’ varied and moving. Meiotic sex offers a means of doing this by shuffling genetic material amongst individuals within a population each generation, despite significant lineage replication-efficiency costs, particularly when some individuals (males) only ever provide genetic material to progeny [9].

In systems dominated by coevolutionary dynamics, there are often significant advantages to rare tactics, which diminish as they become common. Indeed, such so-called negative frequency dependence arises both for the prey of visual predators and the metazoan hosts of microbial parasites. In the latter case, as microbial

pathogens are often clonal, strains that predominate at any given moment are likely to be limited to being resistant to common host defences, and so there is always likely to be a premium on novel, rare host immune tactics [8]. A common tactic adopted by the prey of visual predators is crypsis — the speckled pattern of *typica* peppered moths is cryptic against lichens that predominate on the undersides of branches of unpolluted trees, where individuals rest during the day when avian predators are active [7]. Such coloration is selected for because it makes it more difficult for predators to locate individuals.

Nevertheless, individual predators can ‘get their eye in’ and improve their rate of spotting particular cryptic forms with practice [10]. But whether such ‘search images’ emerge as a result of the development of specific cognitive constructs, as the term suggests, or because individuals learn to search particular micro-habitats more carefully than others [11], this widespread phenomenon places a premium on rare forms, which local predators are unlikely to search for efficiently. Moreover, as cuckoos and their hosts are also subject to strong coevolutionary dynamics, often likened to arms-races, negative

frequency dependence has been hypothesized to be influential in determining host counter-adaptations to brood parasitism [12].

Brood parasites trick others into caring for their young. Cuckoos typically do this by surreptitiously laying their eggs in the nests of other bird species, which provision young with an appropriate diet. Obligate brood parasites, such as the diderik cuckoo, often evolve eggs that mimic the appearance of the eggs of common hosts. This is because a typical host defense is to remove any unusual-looking eggs from the nest when they are noticed [12] — a tactic employed by the African village weaver birds studied by Lahti [1]. It has been suggested that, in such a setting, to make it as difficult as possible for cuckoos to evolve effective egg mimicry, host females should ‘sign’ their eggs [13]. This is because producing variable eggs maximises their rareness, making it unlikely that any local cuckoos will be effective egg mimics; however, merely varying egg appearance also creates a problem for the host female — how does she recognize her own eggs to avoid ejecting them? A potential solution is to produce eggs that differ from those produced by others but that are also consistent for a particular female — eggs that bear her ‘signature’. That way, whether the recognition mechanism is a fixed template coded for by alleles linked to those determining egg characteristics, or if a female learns a ‘search image’ for her own eggs, she minimises the risk of mistaking her own eggs for foreign ones while gaining a rareness advantage.

Although it makes sense as a tactic to cope with brood parasitism, there is little evidence that many typical cuckoo hosts do ‘sign’ their eggs [12]. African village weaver birds, however, display high between-individual variation in egg color and spotting pattern within their typical (cuckoo-ridden) range [14]. And experiments have

demonstrated that individuals will reject the eggs of other weaver birds in proportion to color and spotting pattern differences between foreign eggs and their own [15]. Thus, there is suggestive evidence that ‘egg signing’ may have evolved in this system.

The recent study by Lahti [1] shores up this conclusion by detailing variation in egg appearance — between and within females — in two island populations of African village weavers that have experienced cuckoo-free conditions for known lengths of time, along with similar variation in samples from the two ancestral populations in Africa. Regardless of whether unique aspects of avian vision were accounted for (via spectrophotometer) or not (via color chart matching), this effort demonstrated that color and spotting patterns had become more similar for eggs of different females, yet less consistent for each female’s eggs, on the cuckoo-free islands compared to the corresponding ancestral African populations. These changes were more pronounced for the population that had been cuckoo-free the longest: the Caribbean island of Hispaniola, which had West African weaver birds introduced on it before the 1790s compared to Mauritius in the Indian Ocean, which had birds introduced from South Africa in 1886.

In this way, then, Lahti [1] reports strong circumstantial evidence for the notion that consistent individual differences egg appearance can be selected for by the risk of brood parasitism by cuckoos, at least in African village weaver birds. Indeed, the documented changes are likely to be evolutionary since there is independent evidence that egg appearance is under maternal control [16], is consistent over her lifetime in *P. cucullatus* [17], and eggshell color and patterning have been shown to be genetically determined [18] and independent of diet [19] in other bird species. Thus, it appears that the African village weaver introductions may

offer another clear example of natural selection leading to evolutionary change. To confirm this, however, further work must be done to demonstrate that consistent individual differences in egg appearance are effective in facilitating the recognition of diderik cuckoo eggs by weaver birds, at least in their ancestral range. For, if we can demonstrate that ‘egg signing’ works as an anti-cuckoo tactic, perhaps this will provide general insight into the role of individuality as a means of coping with any sort of parasitism. Further to that, it would be nice to add another easy-to-recognize brick to the wall of evidence for evolution by natural selection as ‘fact’.

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## Carbon Sequestration: Photosynthesis and Subsequent Processes

The increase in the global atmospheric CO<sub>2</sub> concentration projected for 2050 increases the productivity of temperate forests by a quarter; but it is by no means clear that such increased productivity will lead to more long-term carbon sequestration.

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Man's activities have increased, and will continue to increase, the fraction of the atmosphere composed of CO<sub>2</sub>. From values of about 280 μmol mol<sup>-1</sup> between the end of the last glaciation and about 1750, atmospheric CO<sub>2</sub> has increased to about 380 μmol mol<sup>-1</sup> today, and the value in 2050 will be about 550 μmol mol<sup>-1</sup>. Small-scale experiments show that these higher CO<sub>2</sub> levels increase the rate of photosynthesis and plant productivity. Field enrichments with CO<sub>2</sub> also show increases in plant productivity. In a recent paper, Norby *et al.* [1] report a meta-analysis of four Free Air Carbon dioxide Enrichment (FACE) studies on temperate forests. They conclude that the primary productivity of these communities at predicted 2050 CO<sub>2</sub> levels is 23 ± 2% (median ± error derived from regression analysis) higher than at today's CO<sub>2</sub> level; however, such increases in productivity do not necessarily mean an increase in long-term sequestration of carbon.

We need to know how plants will respond to the inevitable increase in CO<sub>2</sub> over the next few decades and beyond. Such knowledge is important in understanding the influence of global environmental change on plants and the biota dependent on them, and is needed to analyze the role of vegetation in

sequestering part of the anthropogenic input of CO<sub>2</sub> to the atmosphere. About half of the CO<sub>2</sub> released since 1750 remains in the atmosphere, with much of the rest sequestered in the ocean and the remainder sequestered in terrestrial ecosystems for periods of decades to centuries [2,3]. With an estimated 60% of terrestrial carbon stored in forest ecosystems [4], it is vital that we get indications of whether such terrestrial sequestration will continue with further increases in CO<sub>2</sub> production.

We need FACE experiments because work in growth cabinets can never really mimic the real world environment either in variability or scale. FACE experiments permit comparisons to be made between present day conditions and the predicted CO<sub>2</sub> level for 2050 (or whenever) for natural stands of vegetation. Initially confined to low-growing vegetation (pastures or arable crops), FACE experiments have subsequently been extended to forests [1]. FACE experiments involve a ring of CO<sub>2</sub>-release points; points are activated depending on wind speed and direction. This enables the experimenter to maintain the required mean CO<sub>2</sub> level, although there can be changes in CO<sub>2</sub> concentrations of 200–300 μmol mol<sup>-1</sup> over periods of 5–20 s [5].

The results of experiments in which such fluctuations were mimicked in controlled environment conditions in

comparison with the same, invariant, mean CO<sub>2</sub> concentration showed that the fluctuating environment in FACE experiments could significantly under-estimate the effects of steady increased CO<sub>2</sub> concentrations [5]. There is also the problem that some FACE experiments economize on CO<sub>2</sub> by not applying CO<sub>2</sub> enrichment at night, although non-photosynthetic effects of CO<sub>2</sub> (on respiration) may not be as large a problem as was initially thought [6,7]. Despite these problems, FACE is rightly the method of choice for studying the effect of enhanced CO<sub>2</sub> on terrestrial communities.

Perhaps the most surprising outcome of Norby *et al.*'s [1] meta-analysis is the consistency among the four studies in the degree of stimulation of productivity by increased CO<sub>2</sub>. This similarity occurred despite differences in tree species, including evergreen conifers and annually deciduous dicotyledons, absolute productivity, soil type, age of the stand, and local climate. The independence of absolute productivity is important: to the extent that it is imposed environmentally rather than by tree genotype, it is consistent with demonstrations that enhancement of productivity by augmenting CO<sub>2</sub> can occur even when productivity is constrained in the present atmosphere by the availability of some other resource [3,8].

Gifford [8] specifically addressed limitation by water supply in semi-arid and arid areas, and by the supply of photosynthetically active radiation in the humid tropics, in modelling the response of global terrestrial productivity to increased CO<sub>2</sub>. Future work could profitably integrate CO<sub>2</sub> effects with the change from nitrogen to phosphorus limitation with time after colonization of 'new'