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Ornamental plumage does not signal male quality in red-billed queleas

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Sexually selected ornaments often function as condition-dependent signals of quality (or 'indicators'). When ornamentation is costly, only high-quality individuals can afford to produce the most elaborate signals. The plumage ornamentation of male red-billed queleas, *Quelea quelea*, is an ideal candidate for an indicator because it is continuously variable, conspicuous, sexually dimorphic, is displayed only during breeding and is partially based on carotenoid pigmentation. However, I show here that quelea plumage is not an indicator because first, plumage colour is not correlated with physical condition or age; second, plumage colour is a genetically determined phenotype that is unresponsive to environmental variation; third, different plumage characters have bimodal distributions; fourth, plumage characters vary independently of one another; and finally, plumage colour is not correlated with reproductive success. To my knowledge, this is the first demonstration of non-condition dependence in colourful and sexually dimorphic breeding ornamentation. Instead, plumage variation may function as a sexually selected signal of individual identity among territorial males that nest in huge, densely packed and highly synchronized colonies.

Keywords: sexual selection; quality signalling; indicators; carotenoids; *Quelea quelea*; individual recognition

1. INTRODUCTION

The idea that sexually selected ornaments function as condition-dependent indicators of quality (or 'indicators'; Andersson 1994) has received much of its support from studies of both carotenoid- and melanin-based plumages (for carotenoids, see Hill 1991, 1992; Hill & Montgomerie 1994; Gray 1996; Camplani *et al.* 1999; Wolfenbarger 1999; McGraw *et al.* 2001; for melanins, see Rohwer & Rohwer 1978; Møller & Erritzøe 1988; Veiga & Puerta 1996; Griffith *et al.* 1999). Competitive-signalling theory assumes that variation in these traits must be correlated with some kind of cost if the traits are to signal reliably the overall phenotypic and genotypic constitution of their bearers (i.e. their quality) (Zahavi 1977; Kodric-Brown & Brown 1984; Grafen 1990; Andersson 1994). The hypothesized costliness of carotenoid-based indicators has drawn much recent interest because animals need to acquire these pigments from their diet (Kodric-Brown & Brown 1984; Gray 1996; Olson & Owens 1998; Hill 1999). If high-quality individuals can afford to sequester, metabolize and deposit more carotenoids into their plumage, then these individuals will also be the most brilliantly coloured (Gray 1996; Olson & Owens 1998; Hill 1999). The costs associated with melanin-based indicators are less clear because animals can synthesize these pigments *de novo* (Gray 1996; Veiga & Puerta 1996). However, there is evidence that both social and physiological costs may be involved in the maintenance and production of melanin-based indicators (Rohwer & Rohwer 1978; Veiga & Puerta 1996, Senar 1999).

The sexually dimorphic breeding plumage of red-billed queleas, *Quelea quelea*, comprises both carotenoid- and melanin-based ornamentation. During the non-breeding season, these abundant African weaver birds are sexually monomorphic and drab brown. However, for breeding, males moult into a brightly coloured plumage comprising two unusually variable features. First, the plumage occurring on the breast and crown ranges in hue from yellow to red and is composed, at least in part, of carotenoid pigments (a yellow pigment is currently unidentified and two red pigments are the carotenoids astaxanthin and α-doradexanthin (R. Stradi, E. Pini and J. Dale, unpublished data; identification techniques are in Stradi *et al.* (1998)). Second, the plumage forming a mask on the face ranges in shade from black to white and is composed of melanin (Ward 1966). In this study, I test the hypothesis that these two characters function as indicators of quality.

(a) *Predictions*

If male quelea plumage is a quality indicator then it should satisfy five conditions. First, plumage characters should be correlated significantly with indices of quality, such as phenotypic condition, size, testes volume and age (Kodric-Brown & Brown 1984; Møller & Erritzøe 1988; Andersson 1992; Hill 1992; Jones & Montgomerie 1992; Andersson 1994; Hill & Montgomerie 1994; Møller 1994; Veiga & Puerta 1996; Griffith *et al.* 1999). Second, expression of characters should have a high degree of environmental determination (Kodric-Brown & Brown 1984; Hill 1992; Andersson 1994; Møller 1994; Griffith *et al.* 1999) since environmental effects (like quality of diet or exposure to disease) should strongly influence an individual's overall quality. Third, each plumage character should have a unimodal frequency distribution (this is not an absolute requirement for a quality indicator, however unimodal distributions are almost always observed in indicator traits in other species (Møller & Erritzøe 1988; Andersson 1992; Hill 1992; Møller 1994; Wolfenbarger 1999; see Senar (1999) for an exception) and they presumably arise from unimodal distributions in the overall quality underlying the traits). Fourth, different plumage characters should be positively correlated with one another (Kodric-Brown & Brown 1984; Hill 1992;

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Camplani *et al.* 1999) (this prediction assumes that the different characters reflect, at least in part, some common aspects of quality (such as overall vigour)). Finally, plumage colour should be correlated with reproductive success (Andersson 1994; Møller 1994; Wolfenbarger 1999; McGraw *et al.* 2001).

I report here that in populations of queleas occurring in Zimbabwe, male nuptial plumage colour does not satisfy the above conditions and therefore is not an indicator of quality. To my knowledge, this is the first demonstration of non-condition dependence in colourful and sexually dimorphic breeding ornamentation.

2. METHODS

(a) *Colour scoring*

For most analyses, I obtained colour scores by taking photographs of specimens and analysing the digitized images with Adobe Photoshop$^{\mathrm{TM}}$ v. 3.0 (Adobe Systems, Inc., San Jose, CA, USA), an imaging software package that gives quantitative scores for any colour in terms of hue, saturation and brightness (see also Kilner & Davies 1998). Photographs of the dorsal and ventral sides of each specimen were taken using flash photography under standardized conditions (in a darkened room, using Kodak Ektachrome 100 film (Eastman Kodak Co., Rochester, NY, USA) with a Nikon P30T camera (Nikon Corporation, Tokyo, Japan) and a Tokina AF 70–210 mm lens (Tokina Co., Ltd, Tokyo, Japan) (set at 90 mm) focused on the birds at a distance of 1.2 m). Photographs were digitized by Kodak onto a Kodak Photo CD. I confirmed that colours were consistent between images by measuring five colour standards included in each photograph. 'Breast hue' was measured at the centre of the breast with Photoshop's colour-picker function. 'Mask shade' was the median greyscale value measured at the centre of the chin with Photoshop's histogram function. I repeated these measures (taken 'blind') on separate photographs of 36 specimens. These measures had high intraclass correlation coefficients (r_{I}) (Zar 1984) demonstrating that the repeatability for the entire process is extremely good (breast hue, $r_{\mathrm{I}} = 0.97$, $F_{35,36} = 75.0$, $p < 0.0001$; mask shade, $r_{\mathrm{I}} = 0.99$, $F_{35,36} = 238.4$, $p < 0.0001$). Furthermore, ultraviolet–visual spectrometer readings from five specimens (see McGraw *et al.* (1999) for methods) indicate that quelea plumage reflected no ultraviolet from the mask, breast and crown, and that reflectance values (R) were strongly correlated with Photoshop measures (ratio of $R_{\mathrm{yellow}(567\ \mathrm{nm})}$ to $R_{\mathrm{red}(700\ \mathrm{nm})}$ versus breast hue, $r^2 = 0.92$; R_{total} versus mask shade, $r^2 = 0.93$).

In one analysis I include a comparison of physical condition with bill hue in order to provide a contrast to plumage colour. Bill hue was the mean hue measured with Photoshop's colour picker at the centre of the dorsal and ventral sides of the upper and lower bills, respectively ($r_{\mathrm{I}} = 0.78$, $F_{35,36} = 8.2$, $p < 0.0001$).

(b) *Morphological analysis*

I measured large samples of males in order to obtain information about condition dependence, frequency distributions and inter-correlations in plumage characteristics. Samples of males comprised a small subset of birds that were killed in pest-control operations conducted by Zimbabwe's Department of Parks and Wildlife Management. The analysis of correlations between indices of physical condition and plumage was based on all males ($n = 324$) that were mist netted from within a breeding colony (20°30′ S, 32°15′ E) on a single day (18 March 1995). Males were killed in the nets, removed and then kept in a deep-freeze for up to one year before being thawed and photographed for colour scoring. I also measured mass (after the crop was emptied), tarsus length, wing length, bill length and combined testis volume (Dale 2000). The analysis of frequency distributions and inter-correlations between plumage traits was based on all males ($n = 574$) similarly sampled from this same colony over a three-day period (13–15 March 1995) and kept in a deep-freeze for up to two months before being thawed and photographed for colour scoring. Colour and condition did not change with prolonged freezing as measurements on 19 males made before being frozen and again after three years in a deep-freeze were highly repeatable (mass, $r_{\mathrm{I}} = 0.80$, $F_{18,19} = 8.9$, $p < 0.0001$; breast hue, $r_{\mathrm{I}} = 0.92$, $F_{18,19} = 24.1$, $p < 0.0001$; and mask shade, $r_{\mathrm{I}} = 0.88$, $F_{18,19} = 15.6$, $p < 0.0001$).

(c) *Captive studies*

I studied a captive population of queleas in order to obtain information about age dependence, environmental determination and heritability in plumage characteristics. I categorized the plumage of 34 males at natural nests (21°03′ S, 31°53′ E) using binoculars (see § 2(d)). Some of these males ($n = 19$) were also trapped, bled and photographed for paternity testing and colour analysis (see §2(a)), respectively. I hand-raised each male's seven-to-nine-day-old nestlings until fledging. These offspring were then kept in large outdoor aviaries (30 m^3) with millet and water provided *ad libitum*. Their breeding plumages were scored (see §2(a)) every year, for up to three years.

(d) *Reproductive success*

I studied queleas breeding in wild colonies in south-eastern Zimbabwe (21°03′ S, 31°53′ E) in order to obtain information about the relationship between reproductive success and plumage coloration. Using binoculars, I classified the plumage of 731 nesting males as either red or yellow, and either white mask or black mask. I then counted the number of live nestlings in the nest of each male eight days after its eggs had hatched. Data from three field seasons (1995–1997) were pooled for this analysis as there were no significant differences in mean reproductive success between years (ANOVA, $F_{2,730} = 0.93$, $p = 0.39$). Each male has only one nest per colony (Crook 1960) and the rate of extra-pair paternity is *ca.* 5–20% (M. Dallimer, J. Dale, J. Pemberton and P. Jones, unpublished data). Samples of males colour scored with binoculars and then later trapped and photographed had scores that corresponded closely with the colour values obtained using Photoshop (mean breast hue of birds classified as red = 19.8 ± 3.7 (s.d.) ($n = 24$), as yellow = 38.2 ± 5.66 (s.d.) ($n = 17$); mean mask shade of birds classified as black = 29.6 ± 9.2 (s.d.) ($n = 22$), as white = 77.0 ± 9.44 (s.d.) ($n = 19$)).

3. RESULTS

(a) *First prediction*

Contrary to the first prediction, breast hue and mask shade were not correlated with any of the four indices of phenotypic quality: mass standardized by skeletal size, wing length, bill length and combined testis volume (table 1). These commonly used indices of size and physical condition are correlated significantly with secondary sexual ornaments in a variety of species including widowbirds, *Euplectes jacksoni* (Andersson 1992), house sparrows, *Passer domesticus* (Møller & Erritzøe 1988), barn swallows, *Hirundi rustica* (Møller 1994), and auklets, *Aethia pusilla* (Jones & Montgomerie 1992). Here,

Table 1. *Correlations between red-billed quelea plumage coloration and indices of phenotypic quality*

	residual mass[a] ($n = 320$)		wing length ($n = 324$)		bill length ($n = 324$)		testes volume ($n = 283$)	
	r_s	p	r_s	p	r_s	p	r_s	p
breast hue[b]	− 0.08	0.15	− 0.02	0.69	− 0.07	0.20	− 0.08	0.21
mask shade[c]	0.03	0.55	− 0.02	0.72	− 0.02	0.78	− 0.08	0.17
bill hue[b]	− 0.17	0.002*	− 0.08	0.15	− 0.14	0.015*	− 0.07	0.24

[a] Residual mass refers to the residuals of mass regressed onto tarsus length.

[b] Lower hue values correspond to more red, less yellow coloration.

[c] Lower shade values correspond to darker coloration.

*$p < 0.05$.

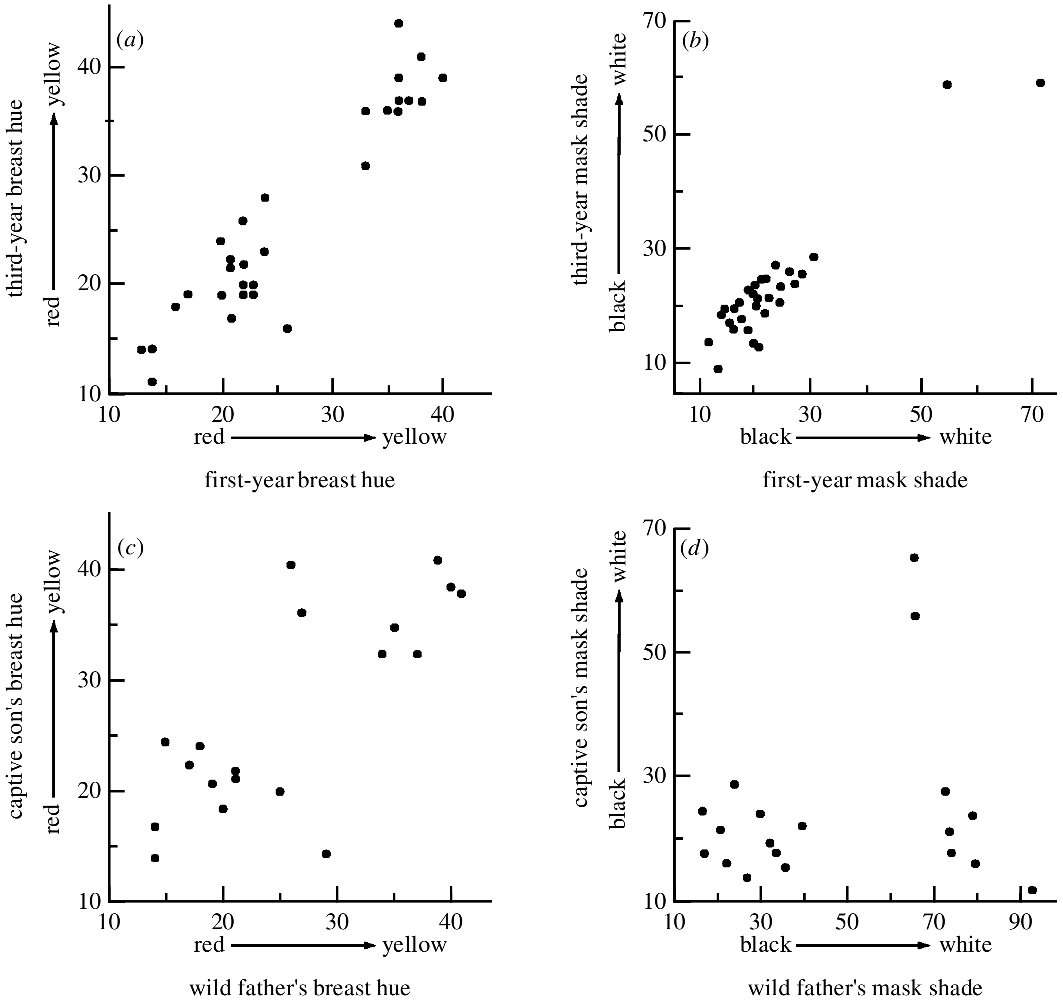

Figure 1. Non-plasticity and genetic determination of quelea breeding plumage. For breast hue, pure red is set at 0 and pure yellow is set at 60; for mask shade, pure black is set at 0 and pure white is set at 100. Correlations among captive males between third-year and first-year (*a*) breast hue ($r_s = 0.86$, $n = 30$, $p < 0.0001$) and (*b*) mask shade ($r_s = 0.78$, $n = 30$, $p < 0.0001$), and correlations between captive son's and wild father's (*c*) breast hue ($r_s = 0.68$, $n = 19$, $p = 0.004$) and (*d*) mask shade ($r_s = -0.06$, $n = 19$, $p = 0.78$). Paternity was confirmed with five polymorphic microsatellite markers (Dallimer 1999) and provided a total exclusionary power of 0.98 (M. Dallimer, J. Dale, J. Pemberton and P. Jones, unpublished data). Plumage scores for captive sons were the mean scores of their first three breeding plumages. Mean brood plumage scores were used in cases ($n = 3$) where a father had two sons in the sample.

however, there were no significant correlations despite analysing a large sample of males caught at the same stage of breeding (quelea colonies are highly synchronized; Crook 1960). In strong contrast to plumage traits, bill hue was a significant predictor of condition for two out of the four indices (table 1). This result, which supports a previous finding that males with redder bills are more dominant in this species (Shawcross & Slater 1983), demonstrates that this analysis would have effectively detected condition dependence in plumage colour were it occurring.

Plumage colour also did not predict age. Captive males moulted into third-year breeding plumages that were nearly identical to their first-year plumages (figure 1*a*,*b*), indicating that a male's plumage coloration is fixed for life.

(b) *Second prediction*

Contrary to the second prediction, the expression of quelea plumage was not environmentally dependent. First, queleas in captivity displayed the same range of hues and shades seen in wild birds (figure 1*c*,*d*), despite being fed an unsupplemented diet of seed only (millet). In other species, carotenoid-based plumages are often duller and more yellow when males are kept in captivity and maintained on diets that are not enhanced with supplementary carotenoids (Thommen 1971; Hill 1992, 1999). Since the captive queleas' diet contained little, if any, of the specific carotenoid pigments they deposited in their plumage, the source of these pigments was probably the metabolic conversion of the yellow carotenoids lutein and/or zeanthin, which were present in their diet in significant amounts (Thommen 1971; R. Stradi, personal communication).

Second, breast hue of captive-raised males was strongly correlated with the breast hue of their wild fathers (figure 1*c*) (parentage of offspring was confirmed with polymorphic microsatellite markers (Dallimer 1999)). The analogous father–son relationship for mask shade was difficult to resolve in this sample due to the small number of white-masked fathers (figure 1*d*). However, I also analysed a sample of 34 fathers that included those above plus an additional 15 putative fathers (parentage not tested molecularly). Here, mask shade of captive-raised males was strongly correlated with that of their wild fathers: white-masked fathers had 47% white-masked offspring and black-masked fathers had 0% white-masked offspring ($\chi^2 = 8.1$, $n = 22$ white-masked and $n = 12$ black-masked fathers, $p = 0.014$). Although indicators are expected to have some degree of father–son similarity (Kodric-Brown & Brown 1984; Hill 1991; Andersson 1994; Møller 1994; Griffith *et al.* 1999), this arises in part through environmental effects (e.g. territory quality), and/or pleiotropic effects of inherited viability genes (e.g. alleles that confer resistance to current strains of pathogens). In contrast, the similarity between captive sons and wild fathers reported here, coupled with evidence of a low degree of phenotypic plasticity (figure 1*a*,*b*), suggests that quelea plumage has a high degree of genetic determination that is based on alleles inherited at polymorphic loci that code directly for plumage colour. For example, a Mendelian model for the white- or black-mask polymorphism, with black masks being homozygous recessive, predicts white-masked fathers will have 55% white-masked offspring and black-masked fathers will have 7% white-masked offspring ($p = 0.07$, $q = 0.93$, Hardy–Weinberg assumptions). These proportions are similar to the proportions observed among the 34 fathers above ($\chi^2 = 1.48$, $p > 0.10$), although other genetic models are also supported.

(c) *Third prediction*

Contrary to the third prediction, both breast hue and mask shade had bimodal frequency distributions (figure 2*a*,*b*). Although variation is continuous, these distributions support Ward (1966) who categorized queleas into broad colour classes (or 'morphs') comprising either red- or yellow-hued males and either black- or white-masked males.

(d) *Fourth prediction*

Contrary to the fourth prediction, breast hue and mask shade assorted independently of each other (figure 2*c*).

(e) *Fifth prediction*

Contrary to the fifth prediction, plumage colour was not correlated with reproductive success as measured by the number of live nestlings a male had in his nest eight days after hatching (two days prior to when nestlings begin leaving their nests) (figure 3). In studies of other socially monogamous species, the number of putative offspring that survive in a male's nest has been found to be correlated significantly with ornamental plumage (Møller 1994; Wolfenbarger 1999; McGraw *et al.* 2001).

4. DISCUSSION

The overall patterns of quelea plumage coloration reported here are different from the general patterns observed in ornamental plumage coloration in other species of birds. For example, coloration in house finches, *Carpodacus mexicanus*, (a commonly cited indicator trait; Olson & Owens 1998) provides a striking comparison to queleas. Both species have carotenoid-based plumages that are remarkably similar in overall appearance. Yet house-finch plumage is unlike quelea plumage because first, it is significantly correlated with a variety of condition indices (Hill & Montgomerie 1994; G. Hill, personal communication) and age (Hill 1992); second, it has a high degree of environmental determination, converging to a drab yellow coloration when males receive a seed-only diet (Hill 1992); third, it has component characters that are unimodally distributed (Hill 1992) and that are significantly correlated with each other (Hill 1992); and finally, it is significantly correlated with reproductive success (McGraw *et al.* 2001). In strong contrast, quelea coloration appears to be a fixed, genetically determined trait, the expression of which is independent of condition. Since there was no support for any of the five predictions based on the indicator hypothesis, it is extremely unlikely that breast hue or mask shade function to signal male quality in queleas.

In this study, I have focused on breast hue and mask shade because these two characters are the most conspicuous and variable features of male plumage (Ward 1966). It is possible that other parameters of plumage colour could be relevant quality-signalling cues. However, in a more detailed morphological analysis (Dale 2000), the condition indices used here (table 1) were not correlated with five additional aspects of plumage coloration: breast saturation (the purity of the carotenoid-based pigmentation on the breast); breast brightness (the lightness of the carotenoid-based pigmentation on the breast); patch size (the area of carotenoid-based pigmentation on the breast and belly); crown hue (the hue of the carotenoid-based pigmentation on the crown) and mask length (the distance that the face mask extends on the crown beyond the base of the bill). Furthermore, there was no indication that plumage coloration was a predictor of condition when the analyses were restricted to within different 'morphs' (e.g. within birds classified as 'red') (Dale 2000).

Little is known about the nature of female choice for male traits in red-billed queleas. There are two predictions

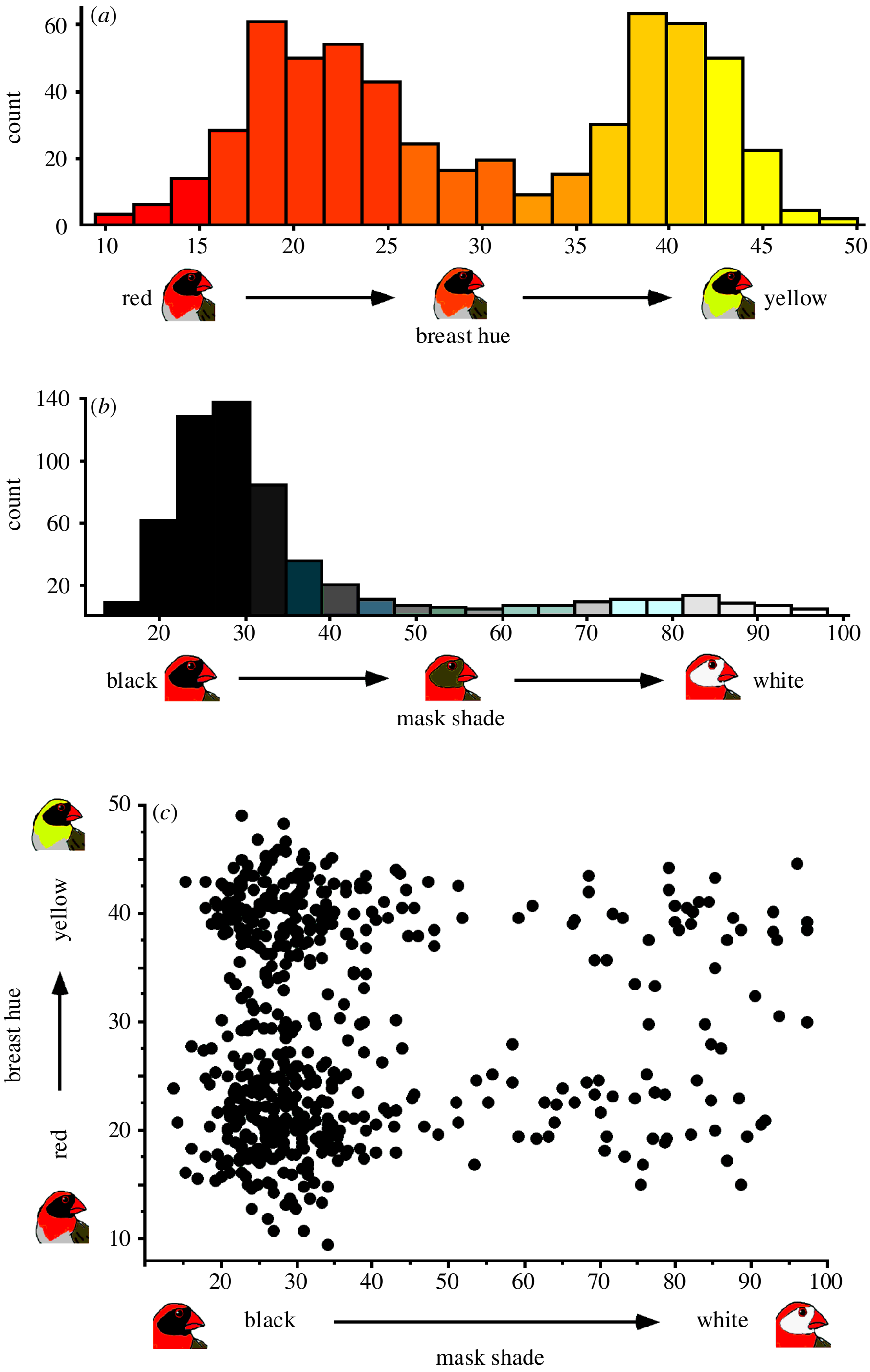

Figure 2. Variation in quelea plumage coloration. (*a*) Breast hue and (*b*) mask shade were continuously variable, had bimodal distributions and (*c*) were not significantly correlated with each other ($r_s = 0.003$, $n = 573$, $p = 0.93$). Males were sampled from a single breeding colony.

about female mating preferences that can be made in light of the results presented here. First, there should be no directional female choice on plumage coloration because ornamental plumage does not signal quality in this species. Second, in contrast to plumage, there should be strong directional female choice for males with redder bills (e.g. as occurs in zebra finches, *Taenopygia guttata*; Burley & Coopersmith 1987) because bill hue does appear to be an indicator of male quality (table 1; see also Shawcross & Slater 1983).

(a) *An alternative hypothesis: signalling individual identity*

If quelea plumage is not a quality indicator, then what alternative function does it serve? It is unlikely that plumage variation is selectively neutral because it is a very conspicuous phenotype that is present only in breeding males. Moreover, variation occurs on the parts of males most visible during social interactions (i.e. the face, crown and breast), suggesting that it functions as a signal.

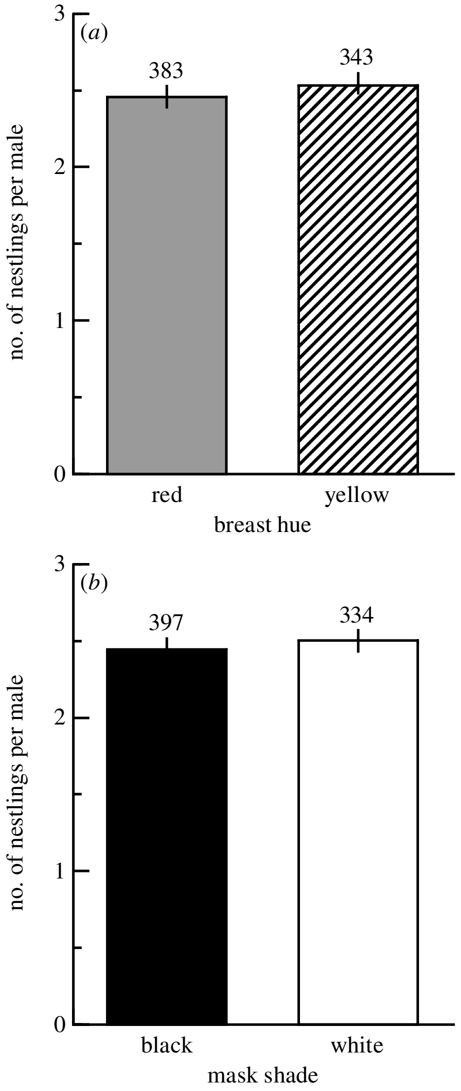

Figure 3. At wild colonies monitored during three breeding seasons, the mean number of nestlings in each male's nest did not differ significantly between (*a*) red-hued (mean = 2.44 ± 1.11 (s.d.)) and yellow-hued males (mean = 2.52 ± 1.07 (s.d.)) ($t = 0.95$ and $p = 0.34$) or (*b*) between black-masked (mean = 2.45 ± 1.11 (s.d.)) and white-masked males (mean = 2.50 ± 1.09 (s.d.)) ($t = 0.63$ and $p = 0.53$). Sample sizes (numbers of nests) and standard errors are given with each bar. Colour groupings correspond to the bimodal distributions evident in figure 2.

A promising possibility is that quelea plumage is a sexually selected signal of individual identity (Wilson 1975; Beecher 1982; Whitfield 1986, 1987; Dale *et al.* 2001). The unique breeding system of queleas is one where individual recognition probably plays an important role. First, quelea males aggressively defend small territories around their nests (Crook 1960). Second, colonies are sufficiently fast paced and synchronous that nest building is initiated and completed by males *en masse* over the course of only three days (Crook 1960); therefore, males form their territories concurrently with numerous nest neighbours in a very short time-period. Third, high breeding density (nests are often in physical contact; Crook 1960) results in males defending territories that overlap with the territories of their neighbours (Dale 2000). Finally, colonies are immense (sometimes numbering millions of nesting pairs; Crook 1960) and so social interactions, including aggression and territorial defence, can occur among huge numbers of individuals. Indeed, neighbouring territorial males clearly recognize each other (Crook 1960; Dale 2000; but see Shawcross & Slater 1983) and tolerate familiar individuals much closer to their nests than unfamiliar birds, who are 'fiercely attacked' (Crook 1960). This suggests that disputes between neighbouring males can be reduced through accurate neighbour–stranger or 'dear enemy' (Wilson 1975) recognition. Individual recognition via visual cues would be particularly effective in queleas because neighbours are in close visual contact. By signalling their individuality visually, males are able to broadcast their identity constantly while simultaneously pursuing other critical activities such as nest building and courtship. If recognition decreased neighbour harassment and increased time devoted to nest building, then recognizable males could have higher mating success because females appear to pay close attention to the nests of their suitors (Crook 1960).

An efficient way to signal identity is to have distinctive cues (i.e. conspicuous traits with high population variance) (Beecher 1982; Whitfield 1986, 1987; Dale *et al.* 2001) based on multiple characters (Beecher 1982) that are not correlated with each other (Beecher 1982; Dale *et al.* 2001) and are cheap to produce (i.e. not dependent on the condition of their bearers) (Dale *et al.* 2001). The patterns of quelea plumage outlined here exhibit precisely these signal properties. In addition, selection for recognizability is likely to be negatively frequency dependent (Dale *et al.* 2001), a form of selection that can readily result in polymorphisms (Maynard Smith 1982) and that is consistent with the observed bimodality of quelea plumage characters (figure 2*a*,*b*).

5. CONCLUSION

The results presented here refute the hypothesis that quelea plumage is a quality indicator and suggest, instead, that it may function as a signal of identity. This study provides a dramatic exception to the idea that variation in conspicuous coloration must be correlated with high and differential costs.

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As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.