FUNCTIONAL SIGNIFICANCE OF ORNAMENTAL PLUMAGE IN RED-BILLED QUELEAS (QUELEA QUELEA)

A Dissertation
Presented to the Faculty of the Graduate School
of Cornell University
in Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy

by
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May 2001


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FUNCTIONAL SIGNIFICANCE OF ORNAMENTAL PLUMAGE IN RED-BILLED QUELEAS (QUELEA QUELEA)

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Cornell University 2001

Sexually selected ornaments often function as condition-dependent signals of quality (or “indicators”). When bright coloration is costly, only high quality individuals can afford to have the most elaborate signals. The plumage coloration of red-billed queleas *Quelea quelea* (Ploceidae) has all the hallmarks of a quality signal because it is highly variable, conspicuous, sexually dimorphic, and is displayed only during breeding. However, in this study of queleas breeding in Zimbabwe, I show that plumage is not an indicator because 1) plumage color does not correlate with physical condition or age, 2) plumage color is a genetically determined phenotype that is unresponsive to environmental variation, 3) different plumage characters have bimodal distributions, 4) plumage characters vary independently of one another, and 5) plumage color does not correlate with reproductive success. This is the first demonstration of non-condition dependence in colorful and sexually dimorphic breeding ornamentation.

If quelea plumage is not a quality signal then what alternative function does it serve? The most promising explanation is that plumage variation may function as a signal of individual identity among territorial males that nest in huge, densely packed and highly synchronized colonies. By having unique plumage patterns, males might be more easily recognized by territorial nest neighbors, resulting in a reduction of aggression received during nesting.

Males aggressively defend areas around their nests, but since nesting density is high, the defended areas of neighboring males overlap. I show that focal males tolerated neighboring males much closer to their nests than they did unfamiliar males. This suggests that disputes over mutually defended areas can be significantly reduced through accurate neighbor-stranger recognition. Moreover, using a mathematical model I argued that signal characters resulting from selection on individuals to be recognizable will (1) be highly variable, (2) often display polymodal distributions, (3) not be condition dependent (i.e. be cheap), (4) not be associated with fitness differences, (5) exhibit independent assortment of component characters, and (6) often occur as fixed phenotypes with a high degree of genetic determination. These are the properties that I observed in the plumage characters of queleas. Furthemore, on the basis of this model, I argued that the ornamental plumage of Ruff Sandpipers *Philomachus pugnax* might also function as a signal if individual identity.

BIOGRAPHICAL SKETCH

Jim Dale was born in Kitwe, Zambia; but grew up in the wilds of Montreal, Quebec after his family immigrated to Canada when he was three years old. Jim received his undergraduate degree in biology at Queen's University in Kingston, Ontario. Mid-way through this degree Jim spent a year in Zimbabwe working as a volunteer field ornithologist for the Zimbabwe Dept. of Parks and Wildlife. After returning to Canada and finishing his undergraduate degree, Jim moved to Ithaca, N.Y. and started his Ph.D in behavioral ecology at Cornell University.

Dedicated with all my love
to my mother and father,
Judith & Peter

ACKNOWLEDGMENTS

I am so happy to have had the opportunity to have studied queleas for my doctorate at Cornell. I thank the board Members of the Malilangwe Trust for permission to work at the Malilangwe Private Wildlife Reserve; and the Whittalls for permission to work at the Save Conservancy. I am particularly indebted to Malilangwe where I have always been made to feel so welcome. Being able to work so much at such a beautiful place has been an unforgettable experience. Thanks so much to Peter J. Mundy for getting me started in bird research in Zimbabwe, pointing me in the direction of queleas and for always being there with help and ideas. Truly wonderful to have met you. For help in the field, thanks to Jeremy Anderson, Ngoni Chiweshe, Ron Hartley, Jeremy Smith, Colin Wynham, Susan and Mavis Mango, Paul Mdondo, and Gavin Young and all the staff at Malilangwe Trust. Thank you very much to Peter Fogarty for painting the truly beautiful frontispiece.

My parents, Peter and Judith, made this all possible. Not just for the obvious reasons such as letting me slowly demolish their Suzuki Samurai on the back roads of Zimbabwe's wild areas, or for letting me build large aviaries in their backyard. But also for happily helping me all along as I pursued what they must have considered a slightly eccentric choice for a career. My Mom once opened up her deep-freeze to find it full of bags of frozen queleas. "My son, the doctor", she said.

Thanks so much to my supervisors Stephen T. Emlen and Paul W. Sherman for their intellectual support, their emotional support, frequent paternal advice and their great friendship. I can't find the words to express my gratitude. I have similar feelings of gratitude to H. Kern Reeve, who really played the role of supervisor number three. And great thanks to my other two committee members David Winkler and Ron Hoy for such terrific ideas and encouraging support. What an awesome committee! It's been an honor to have had the opportunity to get to know all of you.

Financial support came from various teaching assistantships and travel grants from the Cornell Graduate School, the Exploration Society, a Walter E. Benning Scholarship, and an NSF operating grant to Hudson Kern Reeve.

Thanks to my collaborators (and ex-"Shemlen" students) David B. Lank (Chapter 4 & 5) and Hudson Kern Reeve (Chapter 4). Thanks to M. Dallimer for performing the paternity analysis (Chapter 2); R. Stradi for identifying the carotenoid pigments (Chapter 3); and K. McGraw and G. Hill for the spectrometer readings (Chapter 3). An endless supply of comments, suggestions and friendly constructive criticism has come from all my friends from Lunch Bunch and beyond. Great thanks especially to Maydianne Andrade, P.J. Jones, Bob Montgomerie, Geoff Hill, Kevin Mcgraw and Susan Cain. Thanks to my lab-mates Peter Wrege and Pete Buston for providing such a friendly atmosphere and an onslaught of great ideas and suggestions. Great thanks to NB & B's fantastic administrative staff: Terri Natoli, Stacey Coil, Lori Miller, Louise Gunn and Dawn Potter were all so friendly no matter what kind of problem I threw their way (and there were many).

Pappy sure has had a blast hanging out with all the different friends he's made along this journey. Dave Able, Bill Baird, Bruce Carlson, Beth Christman, Jerry Dog, Dan Drecktrah, Ham Farris, Paul Faure, Lauren French, Christy Foran, Jackie Grant, Vik Iyengar, Jill Mateo, Charles Ross, and Matt Weeg, just to name a few. And thanks so much to Liz Tibbetts for everything.

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Introduction:

Diversity fascinates biologists. Indeed, it is the incredibly diverse array of organisms that this planet is teeming with, that led Darwin to his theory of natural selection: those varieties that are the best equipped to survive and reproduce will pass on their characteristics disproportionately more so into the next generation (Darwin 1859). Natural selection depends on variation in a critical way: if there is no variation there can be no selection. Paradoxically, natural selection tends to eliminate the variation that it feeds on, and so what we tend to see at any given moment in geological time, is that most individuals within a species exhibit very similar traits. Consider the coloration of plumage in a typical garden bird, say a blue jay: they all look very similar (that is, variation in plumage color is low). Presumably this is a result of past selection favoring certain plumage patterns over others, with the result that these patterns have become invariable (relatively) in the populations of jays that we see today. In many species of birds, however, plumage color can be quite dramatically variable. Why is it that in these species, natural selection has not resulted in the fixation of that color that is most advantageous in the current social and ecological environment? Well, for the most part, evolutionary hypotheses that attempt to explain the occurrence of high degrees of plumage color variation, essentially argue that it is the *variation* itself that is adaptive. In this chapter I will discuss variation in plumage color in birds through the presentation and review of two major hypotheses to explain it's occurrence. This is not to imply that there are not many other important hypotheses. However, for the purposes of the study species used in most of the research described in this thesis, red-billed queleas *Quelea quelea*, I argue that these two hypotheses standout from the rest as having the greatest promise towards a functional understanding of plumage variation. These two hypotheses are 1) quality signaling, and 2) individual identity signaling.

1) Quality signaling

A commonly invoked hypothesis to explain variation in plumage color in birds is that bright plumage color is an honest indicator of quality. The basic idea is that more brightly colored individuals within a population are expected to be larger, be in better physical condition, have lower parasite loads, be able to maintain and defend higher quality territories, be able to provide more and higher quality food to youngsters, etc. (Zahavi 1975; Kodric Brown and Brown 1984; Grafen 1990; Anderson 1994; Olson and Owens 1998). Plumage coloration is maintained as an honest signal because bright plumage incurs at least one of two possible costs: costs of producing bright color, and costs of having bright color. Costs in the former category would include foraging costs invoked through sequestering possibly rare pigments from the environment, and through increased metabolic costs from pigment production (Kodric Brown and Brown 1984; Olson and Owens 1998). Costs of having bright color could arise from increased predation on bright individuals or through increased intraspecific aggression from other individuals (Rohwer and Rohwer 1978; Whitfield 1987). Only those individuals of high quality should be able to withstand the costs of producing and/or having bright coloration. The result of this is that the any degree of plumage color variation seen in a population stems from variation in the overall quality of the individuals in that population.

Selection for signals to be honest could arise through mate choice and/or social interactions. Individuals (females, in general) should be selected to base their mate choices on criteria that are honest signals of quality, such that they could choose the best mate available to them and increase their own reproductive success through indirect benefits (e.g. good genes) or direct benefits (e.g. good parental care) that they gain from high quality mates. Indeed, selection might favor females whose mate preferences involve traits that are not only correlated to male quality but that actually amplify the perceivable differences in male quality such that good quality males are more easily identifiable: the result is very high degrees in variation in the expression of those traits (Alatalo et al. 1978; Kodric Brown and Brown 1984). Secondly, even if a trait is not costly to produce, it might benefit an individual to reliably signal his quality (or status) in order to reduce aggression directed towards them from higher quality individuals (e.g. status signaling (Rohwer and Rohwer 1978; Whitfield 1987)).

A classic study on condition dependent plumage coloration in birds is Geoffrey Hill's work on House Finches (Hill 1991; 1992). House Finch males vary in color from dull yellow to bright red, and the coloration is produced through the acquisition of carotenoid pigments from their diet. Red pigments are thought to be rarer and more difficult to sequester than are yellow or orange pigments, and so those males who are reddest are of high enough quality such that they can expend the extra time and energy needed to get these pigments. Variation in plumage color of wild populations of house finches is high; whereas captive flocks of males fed on constant diets tend to converge onto similar plumage colors and overall variation is reduced considerably (Hill 1992). This suggests that all house finch males carry similar genes for plumage color (that is, they all have the same potential to be bright red), and the degree of expression of those genes will depend on the overall ability of the male to acquire the pigments (Hill 1992). Indeed, females were found to prefer red males as mates over yellow males (Hill 1991), and Hill has uncovered many significant positive correlations between plumage color and various measures of male quality (wing and tail length, mass, "condition" (i.e. mass controlled for by skeletal size), return rate to breeding sites, paternal feeding rates, timing of molt, and feather growth rates (Hill 1991; Hill and Montgomerie 1994; G.E. Hill pers. comm.).

Over the past decade the quality indicator hypothesis has generated widespread support as there is abundant evidence for plumage color being an honest indicator of quality and/or status in many species of birds (e.g. least auklets (Jones 1990), dotteral (Owens et al. 1994), pied flycatcher (Jarvi et al., 1987), cardinals (Wolfenbarger 1996) , Darwin's finches (Grant and Grant 1987), and yellow warblers (Studd and Robertson 1985))

Overall, the quality indicator process will evolve through sexual selection (either intersexual selection where one sex is selected to use honest indicators of quality as their mate choice criteria, or intrasexual selection where individuals of the same sex will be selected to display honestly to each other their ability to compete for mates). However, quality indicators can also be selected for in non-mating situations such as winter feeding flocks where individuals compete for access to limited food supplies. Under such systems, honest indicators of quality (or status) would peovide useful information enabling individuals to avoid unnecessary escalations of conflict: if two birds can peacefully pre-determine who would likely win a contest were it to occur, then perhaps the costs each would incur in the contest itself can be avoided. This would be particularly useful when species form large unstable feeding flocks such that individuals repeatably compete with previously unknown birds (Whitfield 1987).

2) Individual identity signaling

Under certain conditions it will be important for individuals to be able to identify others as being the particular individuals they are (individual recognition). For example, in order to identify kin vs. non-kin (so that altruistic behaviors can be directed towards kin (Beecher 1989)), in order to identify who is who in a dominance hierarchy (so that time- and energy-consuming conflicts can be avoided (Barnard and Burk 1979)); or in order to identify who the owners of neighboring territories are during breeding periods so that potentially agonistic rivals can be correctly discerned from non-threatening neighbors ("dear-enemy" hypothesis (Wilson 1975)). Some examples of individual recognition in the animal kingdom are quite well known: parents in colonial nesting swallows can identify their putative offspring from the characteristics of their begging calls (Medvin and Beecher 1986), dogs can identify different individuals through scent, and many different species of songbirds can discriminate the songs of males in neighboring territories from the songs of strangers (Lambrechts and Dhondt 1995).

Even though recognition can be accomplished through the identification of unique scents, vocalizations or visual appearances of particular individuals; in birds, most known cases of individual recognition occur through variation in vocalizations (Lambrechts and Dhondt 1995). Nevertheless, plumage variation could also be an important cue for recognition. Thus, any selection for the ability to recognize individuals could provide the social environment necessary to lead to an evolutionary increase in plumage variation: those individuals who look unique will have a better chance of being correctly identified and could thus avoid time-consuming, energetically-costly or risky agonistic encounters (Chapter 4).

There are only a handful of examples of possible individual recognition mediated through plumage variation in birds. In breeding Ruddy Turnstones, individuals basically ignored decoys of birds that had markings similar to turnstones in neighboring territories, yet they directed aggression towards decoys with previously unseen plumage patterns (Whitfield 1986). Males in leks of ruff sandpipers will be more aggressive towards males whose plumage has been altered than to sham-controlled males (D. B. Lank, pers. comm.). Within flocks of Harris sparrows and within flocks of White-throated sparrows, there tends to be less overall aggression among groups of more variably-plumaged birds: a result that is consistent with the idea that individual recognition is facilitated by increased plumage variation, (although a similar result would be expected if plumage color is an honest indicators of quality) (Watt 1986). And finally, a fascinating example of possible individual recognition occurring through plumage variation is in the red-legged shag. In this species, it is the recently fledged juveniles that vary in plumage color, feet color, gular pouch color, and the extent of filoplumes on the neck. Parents must locate recently fledged young in creches for feeding, and so the color variation possibly aids adults in correctly identifying their kin (Rasmussen 1988).

Although individual recognition by vocal cues in birds appears to be common, the use of variation in plumage as a cue for individual recognition might also be widespread. An important but difficult question is whether or not selection for increased "recognizability" can result in increases in overall plumage variation in a species., or whether recognition occurs through pre-existing variation caused through other evolutionary forces. The use of plumage color for recognition over the use of sound might be expected in species where individuals are in frequent visual contact (such as in open habitats or in dense breeding colonies), when there are limitations on sound production and/or transmission, under conditions where it is important to broadcast your "individuality" for periods of long duration, and under conditions where it is important to learn who different individuals are quickly. Future studies are badly needed in order to identify the sociological conditions where recognizability is selected for; and what conditions favor broadcasting individual identity in different communication media.

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THE ROYAL SOCIETY

doi 10.1098/rspb.2000.1261

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;

Received 24 May 2000 *Accepted* 1 August 2000

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^{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 grey-scale 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, $r_I = 0.97$, $F_{35,36} = 75.0$, $p < 0.0001$; mask shade, $r_I = 0.99$, $F_{35,36} = 238.4$, $p < 0.0001$). 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 $R_{\text{yellow}(567\text{ nm})}$ to $R_{\text{red}(700\text{ nm})}$ 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 ($r_I = 0.78$, $F_{35,36} = 8.2$, $p < 0.0001$).

(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, $r_I = 0.80$, $F_{18,19} = 8.9$, $p < 0.0001$; breast hue, $r_I = 0.92$, $F_{18,19} = 24.1$, $p < 0.0001$; and mask shade, $r_I = 0.88$, $F_{18,19} = 15.6$, $p < 0.0001$).

(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.
* $p < 0.05$.

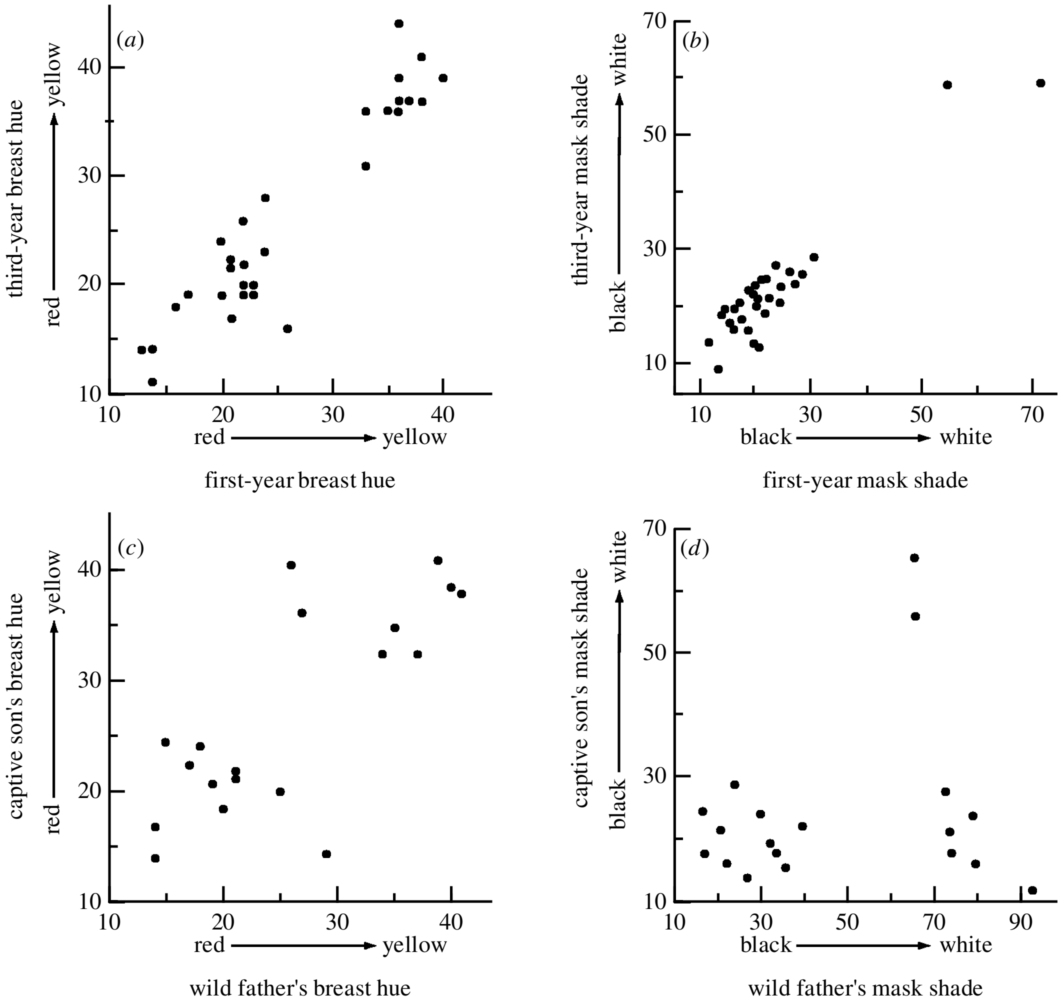

Figure 1. Non-plasticity and genetic determination of quelea breeding plumage. For breast hue, pure red is set at 0 and pure yellow is set at 60; for mask shade, pure black is set at 0 and pure white is set at 100. Correlations among captive males between third-year and first-year (*a*) breast hue ($r_s = 0.86$, $n = 30$, $p < 0.0001$) 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

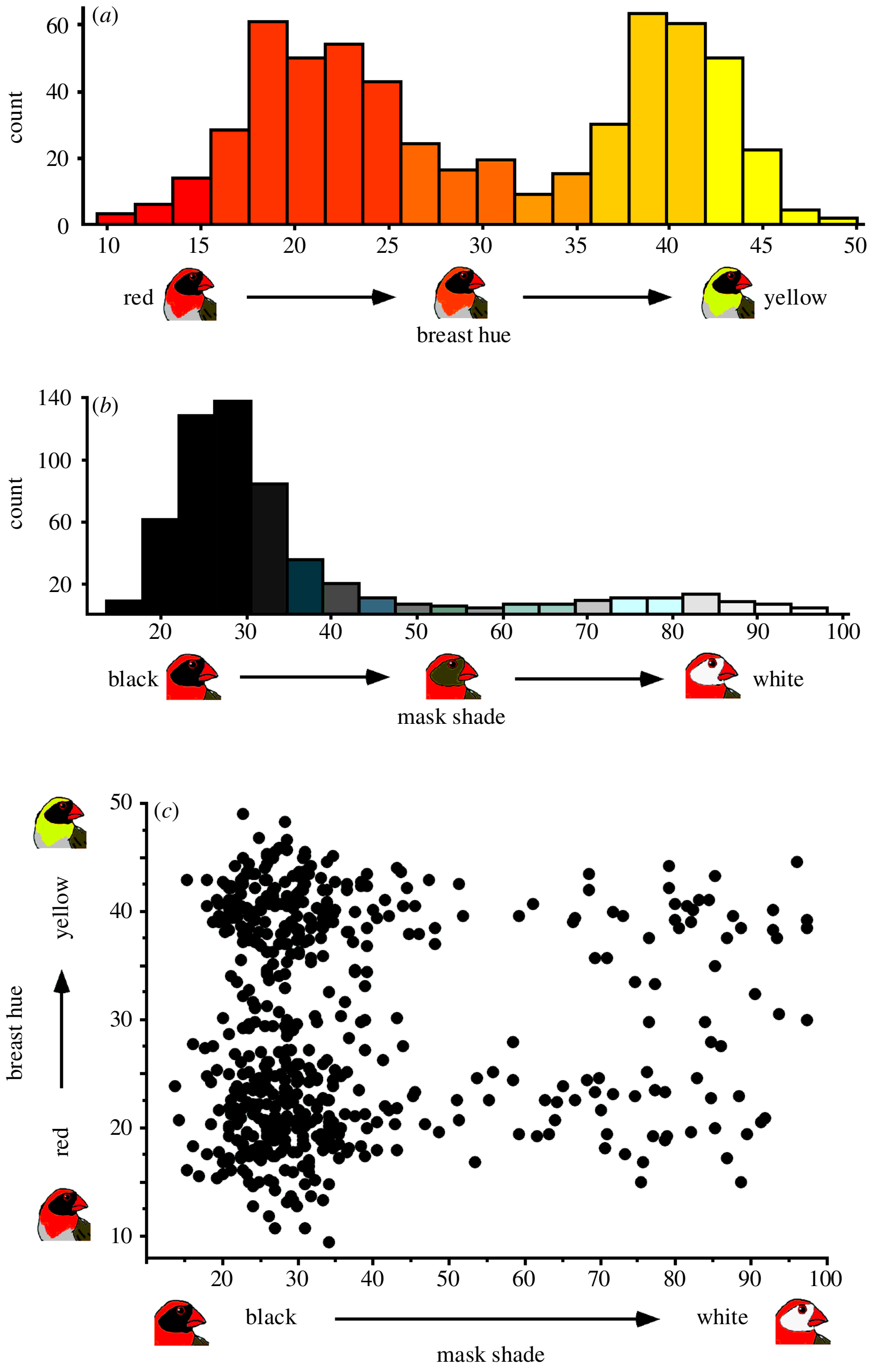

Figure 2. Variation in quelea plumage coloration. (*a*) Breast hue and (*b*) mask shade were continuously variable, had bimodal distributions and (*c*) were not significantly correlated with each other ($r_s = 0.003$, $n = 573$, $p = 0.93$). Males were sampled from a single breeding colony.

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.

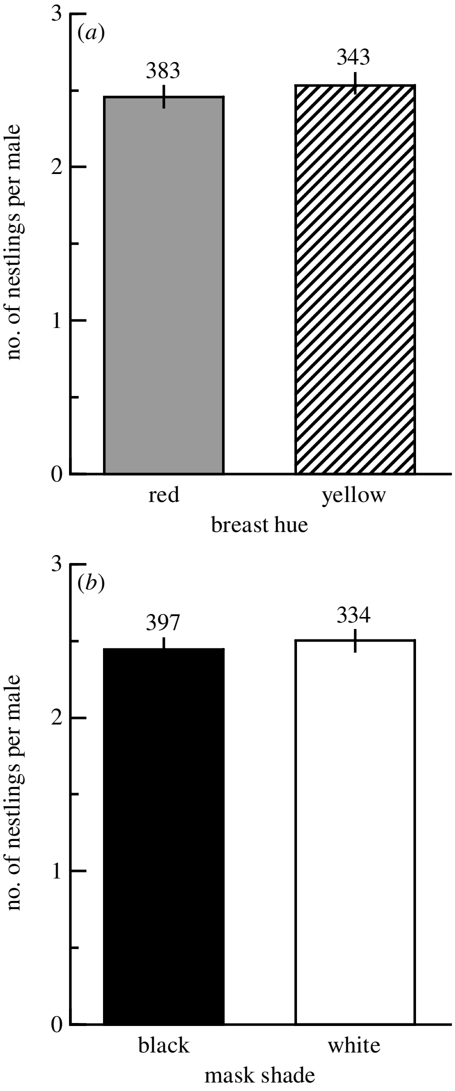

Figure 3. At wild colonies monitored during three breeding seasons, the mean number of nestlings in each male's nest did not differ significantly between (*a*) red-hued (mean = 2.44 ± 1.11 (s.d.)) and yellow-hued males (mean = 2.52 ± 1.07 (s.d.)) ($t = 0.95$ and $p = 0.34$) or (*b*) between black-masked (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.

I thank the Cornell Graduate School and the Exploration Society for support; the Board Members of the Malilangwe Trust for permission to work at the Malilangwe Private Wildlife Reserve; the Whittalls for permission to work at the Save Conservancy (Humani); A. P. Dale and D. J. Dale for a vehicle and aviary space; M. Dallimer for performing the paternity analysis; R. Stradi for identifying the carotenoid pigments; G. Hill's laboratory for the spectrometer readings; R. Hartley, P. Mundy and the staff at Malilangwe for help in Zimbabwe; and P. Buston, A. Dhondt, S. Emlen, D. Lank, P. J. Jones, K. McGraw, R. Montgomerie, H. K. Reeve, P. Sherman, E. Tibbetts, S. Vehrencamp, D. Winkler and P. Wrege for comments on the manuscript. This work was conducted with approval from the Research Council of Zimbabwe, the Zimbabwe Department of National Parks and Wildlife Management and the Cornell Center for Research Animal Resources. This research comprises a portion of my doctoral thesis requirements (Cornell University).

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

CHAPTER THREE:

A functional analysis of plumage polymorphism in red-billed queleas

Summary: There is widespread consensus among behavioral ecologists that the ornamental and sexually-dimorphic breeding plumages of many birds often function as condition-dependent "indicators" of phenotypic and possibly genetic quality. The breeding plumage of red-billed queleas *Quelea quelea* is an ideal candidate for a quality indicator because it is conspicuous and sexually dimorphic. In this study, I present a detailed morphological analysis on 7 highly variable plumage characteristics from a large sample of males captured within a single breeding colony (breast hue, saturation, and brightness, crown hue, ventral patch area, mask shade, and mask length). Breast hue, crown hue and mask shade had bimodal frequency distributions, while the other traits demonstrated unimodal frequency distributions. Breast hue, saturation and brightness were all strongly correlated with each other, however the other plumage features varied (for the most part) completely independently of each other. Finally, none of the plumage traits reliably predicted quality as measured by 10 different indices ranging from phenotypic condition, body size, testes volume, ptilochronology, and crop contents. This remained true even when I checked for correlations within samples of males grouped by broad color classes. These patterns are not consistent with the indicator hypothesis because indicators are expected to have unimodal distributions, demonstrate significant positive correlations with each other, and (most critically) be significantly and positively correlated with measures of quality. I consider 6 more alternative hypotheses to explain variation in quelea

plumage: 1) Neutral mutation, 2) Fisherian runaway selection, 3) Differential microhabitat selection, 4) Kinship signaling, 5) Compatible-mate signaling, and 6) Individual identity signaling. I suggest that out of all of these, the observed patterns of plumage coloration are most consistent with individual identity signaling. This makes sense because colonially-breeding males live in a social environment where being recognizable is likely critical: within cohesive social groups (neighborhoods of nesting males) interacting within a huge assemblage of unfamiliar birds.

Introduction

Animal ornaments, such as gaudily colored bird plumages, have long posed a problem for evolutionary biologists because such features appear costly to produce and / or maintain   At the same time, they offer no obvious survival advantage, and so why should natural selection favor them (Darwin 1879)? Progress towards a resolution of this problem was made through the discovery that ornamental features in many different animals primarily function as condition-dependent, intra-specific signals of overall vigor (hereafter “indicators” sensu Andersson (1994)). During inter- and intrasexual competition, receivers (potential mates or sexual rivals) are expected by theorists to behave favorably towards senders who broadcast their abilities honestly (e.g. by choosing them as mates, or by withdrawing from them during fights). In general as long as variance in ornament expression has differential costs associated with it (through producing or maintaining the ornament), then the degree to which it is expressed should be a reliable indicator of the overall phenotypic and perhaps genetic constitution of its bearer (i.e. its quality) (Zahavi 1977; Grafen 1990; Kodric-Brown and Brown 1984; Andersson 1994; Olson and Owens 1998). Ironically then, animal ornaments are now believed by many to be selected for *because* of their costs, not despite them.

Empirical support for the indicator hypothesis has come from in-depth studies on plumage color variation in a variety of different species. For example in house sparrows *Passer domesticus*, males with larger throat patches are more dominant (Møller 1987), are in better physical condition (Veiga 1993; Veiga and Puerta 1996), breed earlier (Møller 1989), are older (Veiga and Puerta; Griffiths et al. 1999), are larger (Møller and Eritzoe 1988), have larger testes (Møller and Eritzoe 1988) and provide better nest defense (Reyer et al. 1998). There is debate about what kinds of costs are associated with the house sparrow's black bib, but general acceptance that there must be one (Veiga and Puerta 1996; Senar 1999).

Another widely-cited example is the carotenoid-based plumage coloration of house finches *Carpodecus mexicanus*. In this species, males with more red (less yellow) plumage are larger and in better physical condition (G. Hill, pers. comm.), have greater over-winter survival (Hill 1991), molt earlier and faster (Hill and Montgomerie 1994), are less parasitized (Thompson et al. 1997) and provide parental care at higher rates (Hill 1991). The hypothesized costs of carotenoid-based ornaments are argued to stem from the fact that birds must obtain carotenoids from their food (Thommen 1971). Because of this, the pigments are therefore theoretically limiting (for example carotenoids may be difficult to find or energetically demanding to metabolize) (Kodric

Brown and Brown 1984; Gray 1996; Olson and Owens 1998; Hill 1999). As with melanin-based indicators, the specific costs associated with carotenoid expression are still unresolved (Olson and Owens 1998; Hill 1999).

Additional empirical support for the idea that variance in plumage color ornamentation often does reliably indicate aspects of their bearer's quality comes from work on cardinals *Cardinalis cardinalis* (Wolfenbarger 1999a; 1999b), Darwin's finches *Geospiza magnirostris* (Grant and Grant 1987), pied flycatchers *Ficedula hypoleuca* (Jarvi et al. 1987; Slagsvold and Litjeld 1992), blue grosbeaks *Guiraca caerulea* (Keyser and Hill 1999), and many others. Furthermore, there are many other studies on indicators in many signaling systems other than plumage coloration. For example, patterns observed in structural plumage indicators (e.g. long tails, or plumes) are generally similar to patterns observed in plumage color indicators. For example, detailed studies on widowbirds *Euplectes* spp.(Alatalo et al. 1988; Andersson 1992), barn swallows *Hirundi rustica* (Møller 1994) and least auklets *Aethia pusilla* (Jones and Montgomerie 1992) all provide support for the indicator hypothesis.

The studies listed above are testimony to how empirical support for the indicator hypothesis has increased dramatically over the last decade or so. The indicator hypothesis has been so effective at explaining variation in plumage coloration, that in some academic circles, it represents the established paradigm. Occasionally, rather than testing whether plumage color *does* signal quality, researchers use plumage color *as* an index of quality (e.g. Slagsvold et al. 1999). Nevertheless, there is great deal more research to be done before we can arrive at a complete understanding of the colorful plumages exhibited by the world's different species of birds (and of animal ornamentation in general). For example, what other functional hypotheses represent potential explanations of bright plumage coloration in birds? Why are some species much more variable in coloration than others?

Red-billed Queleas

This is a descriptive study of polymorphism in the breeding plumage of red-billed queleas, (Ploceidae: *Quelea quelea*) an infamous and abundant avian agricultural pest of sub-Saharan Africa (Bruggers and Elliott 1989). This monogamously-breeding weaver-bird is well known for reproducing in huge, crowded and highly synchronized colonies. However a less well known, but similarly remarkable, feature of queleas, is the dramatic variability in the colorful plumage that males molt into for breeding. This plumage includes 1) a face mask that is based on melanin pigmentation that varies in shade from white to black, and varies in shape at the top of the head from nothing to a broad stripe, and 2) a carotenoid-based patch of colored feathers that surrounds this face mask and which varies in hue from red to yellow, and varies in area from a small thumbnail-sized patch to the entire breast and belly being fully pigmented. (Ward 1966; Chapter 2; R. Stradi pers. comm.)

In chapter 2, I argued that 2 characteristics of quelea plumage (plumage hue and mask shade) were not signals of quality. In this chapter I expand on that work by 1) evaluating the full range of plumage variability in queleas as measured by 7 different characteristics, 2) performing a more thorough analysis of condition-dependence using 10 different measures of condition and quality which I analyse in multiple ways, and 3) consider a total of 8 alternative functional hypotheses to explain why plumage in this species might be so variable.

Functional hypotheses

Since quelea plumage is conspicuous and colorful, continuously variable, sexually dimorphic (females are drab brown), and present only for breeding (males are similar to females in the non-breeding season), it would seem to be an ideal candidate for a condition-dependent indicator of quality.

Quelea plumage variation is extreme, however, even in comparison to the most variable of plumages believed to function as indicators. It may be that something different is going on in this species, and therefore it is especially appropriate to consider alternative hypotheses concerning the function of quelea plumage coloration. In this paper I consider six additional functional hypotheses: 1) The *Neutral Mutation* hypothesis is that plumage coloration is selectively neutral and thus it evolves only through genetic drift (Falconer 1989). 2) The*Fisherian Runaway* hypothesis argues that plumage ornamentation is the outcome of a genetic correlation between loci coding for the ornamental traits and the loci coding for the female mating preferences for those traits (O'Donald 1983). 3) The *Differential microhabitat selectio*n hypothesis states that different plumage varieties are differentially selected for or against under variable microhabitats regularly occupied by the species as a whole (Hazel and Johnson 1990; Morey 1990). 4) The *Kinship signaling* hypothesis is that plumage reveals the degree of relatedness between different males and that it is used for inducing nepotism from, or avoiding competition with, kin (Petrie et al. 1999). 5) The *Complementary-mate signaling* hypothesis is that plumage is a cue used during mate choice as a basis to assess potential genetic complementarity of a potential breeding partner (Wedekind and Furi 1997). Finally 6) The *Individual identity signaling hypothesis* argues that plumage is a signal of identity that is maintained by selection for individual recognizability (e.g. through avoidance of aggression from territorial neighbors) (Whitfield 1987; Chapter 5).

Based on the data presented here and from further data reviewed from the literature, I argue that quelea plumage coloration is not an indicator of quality. Secondly, of all the above alternative hypotheses, I suggest that individual recognition provides the most promise towards obtaining a functional understanding of the variable plumage of the red-billed quelea. It is clear, however, that future research will be required in order to resolve the question.

Methods

The purpose of this paper is to provide a comprehensive description of the variation observed in the breeding plumage of male red-billed queleas. In order to accomplish this, I present information on three aspects of plumage coloration in queleas: 1) the frequency distributions of different plumage characters, 2) inter-correlations among different plumage characters, and 3) correlations among plumage characters and a wide variety of indices of physiological condition and overall quality.

Study sample.

The analysis of plumage characters presented here is mostly based on detailed morphological measurements made on a sample of 324 male *Q. quelea* that were mist-netted on 18/03/1995 within a single breeding colony in south-eastern Zimbabwe (20˚30'S, 32˚15'E). The birds comprised a small random sample of individuals killed in a routine pest-control operation conducted by the Zimbabwe Dept. of Parks and Wild Life. Birds were killed immediately after capture, and deep-frozen until measured (7 to11 months later). All birds in the sample were males in full breeding plumage and had fully developed testes, indicating they were reproductively active.

Color measurements.

Plumage Color was measured from photographs of the specimens that had been digitized and analyzed with Adobe Photoshop™ Version 3.0 (see also Kilner and Davies 1998), an imaging software package which gives quantitative scores for any color in terms of hue, saturation and brightness. Photographs of the dorsal and ventral sides to each specimen were taken using flash photography under standardized conditions: in a darkened room with a Nikon P30T camera with a TokinaAF 70-210 mm lens (set at 90 mm) focused on the birds at a distance of 1.2 m. I used Kodak Ectachrome 100 Film and, to minimize variation further, different film rolls were all taken from the same batch of 20 rolls of film, and they were all developed professionally, en masse. These photographs were then scanned by Kodak onto a Kodak photo CD. I analyzed color on 384 x 256 resolution images - each bird in these images occupied about 50 x 150 pixels, and there were 9 birds per image. I measured six different plumage characters from these photographs: breast hue, breast saturation, breast brightness, crown hue, ventral patch area, and mask shade. I measured a seventh character, mask length, on the specimens directly (Figure 3.1).

Breast Hue and Crown Hue: I measured breast hue at the center of the breast and crown hue at the center of the crown, using Photoshop's color-picker function (set to measure color from a 5x5 pixel square). Photoshop defines the hue of pure red at 0 and pure yellow at 60 and since plumage hue measurements fell within this range I treated hue scores as an interval-scale variable with lower values indicating redder plumage.

Breast Saturation and Brightness. I measured these characters at the center of the breast with the color picker. Photoshop measures saturation on a scale of 0 to 100, with lower scores indicating paler, less deep, more washed-out colors (for example pink is less saturated than red). Similarly, photoshop measures brightness from 0 to 100, with lower values indicating duller, less vibrant colors (for example, brown is less bright than orange) .

Patch Area. Patch area was measured using Photoshop's lasso tool to outline the patch of colored feathers below the face mask and the number of pixels within this area was determined with Photoshop's histogram function (I transformed pixel number into cm^2 using an area standard included in each photograph).

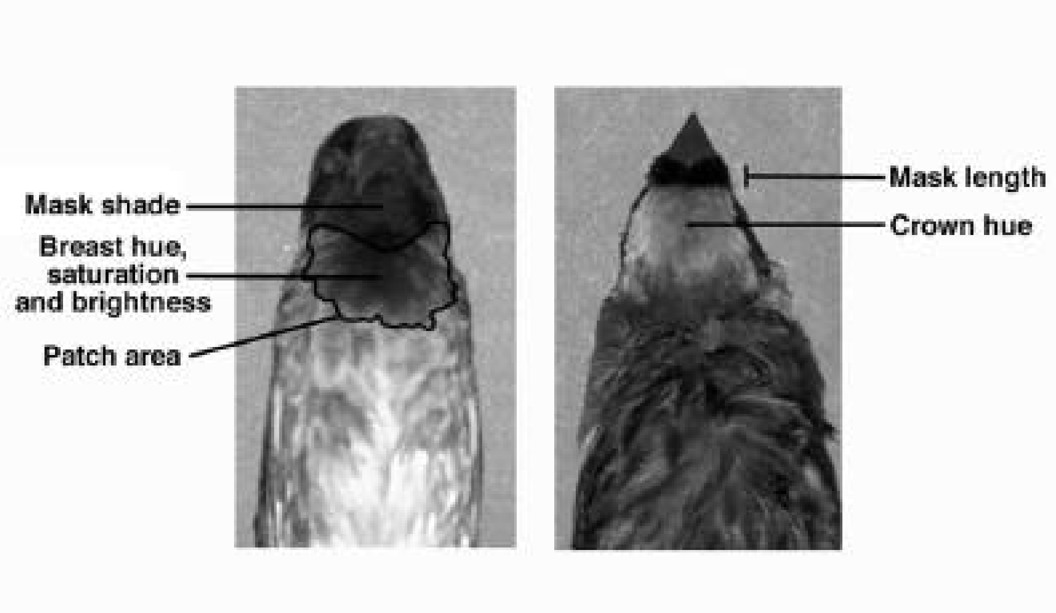

Figure 3.1. The seven different plumage traits analyzed in this study.

Mask shade. I measured mask shade by outlining a small square patch (5x5 pixels) on the throat immediately below the bill using the marquee tool and taking the median grayscale value of this selection with the histogram function. Photoshop sets the grayscale values of pure black at 0 and pure white at 255 and so mask shade was considered an interval-scale variable with lower numbers indicating a darker face-mask (I divided grayscale measures by 2.55 to obtain a scale from 0 to 100).

Mask length. I measured mask length directly off of the specimens with dial calipers and defined it as the length (in mm) that the face mask extended on the crown beyond the base of the bill.

Repeatability of color measurements.

In repeated measures (taken 'blind', using separate photographs) all these measures had high intraclass correlation coefficients (r_I) (Zar 1984) demonstrating that the whole color scoring process is highly repeatable (breast hue: $r_I = 0.97$, $F_{35,36} = 75.0$, $P<0.0001$; plumage saturation: $r_I = 0.90$, $F_{35,36} = 19.0$, $P<0.0001$; plumage brightness: $r_I = 0.94$, $F_{35,36} = 30.1$, $P<0.0001$; crown hue: $r_I = 0.97$, $F_{35,36} = 75.0$, $P<0.0001$ mask shade: $r_I = 0.99$, $F_{35,36} = 238.4$, $P<0.0001$; patch area: $r_I = 0.99$, $F_{35,36} = 148.3$, $P<0.0001$; mask length: $r_I = 0.78$, $F_{35,36} = 8.2$, $P<0.0001$). Moreover, variance in scores for color standards were much lower than variance in the actual plumage scores, indicating that intra-photograph color variation was minor relative to phenotypic variation: variance in standards as a percentage of variance in plumage scores were 0.9% - 5.0% for breast hue (4 standards, N=72 photos), and 7.2% for mask shade (1 graycard standard, N=72 photos). An assumption of this study is that the effects of freezing of the specimens did not result in any of the patterns reported here. Firstly, plumage variation in the thawed specimens appeared to me to be similar to, and as striking as, the variation that is present in live birds. Secondly, as far as I know, freezing birds is not known to result in changes in plumage coloration. Finally, measurements of plumage color and mass were highly repeatable among 19 males measured before being frozen and then again after three years in deep freeze (mass: r_I = 0.80, $F_{18,19}$ = 8.9, P<0.0001; plumage hue: r_I = 0.92, $F_{18,19}$ = 24.1, P<0.0001; and mask shade: r_I = 0.88, $F_{18,19}$ = 15.6, P<0.0001; other variables not measured).

UV reflectance.

Many birds are capable of seeing in the UV range of the electromagnetic spectrum, and so color based on UV reflectance may play an important role in avian visual communication (Andersson and Amundsun 1997; Keyser and Hill 1999). In queleas however, UV-visible spectrometer readings (McGraw et al. 1999) from 5 specimens (Figure 3.2) indicate that there is little to no UV reflectance off of plumage (mask, breast and crown). Furthermore, reflectance values (R) correlate strongly with Photoshop measures (ratio of $R_{yellow\ (567nm)}$ to $R_{red\ (700\ nm)}$ vs. breast hue, r^2 = 0.92; R_{total} vs. mask shade, r^2 = 0.93), indicating that the photoshop technique used here for measuring color variation essentially captures the same information as does UV-vis spectrometry.

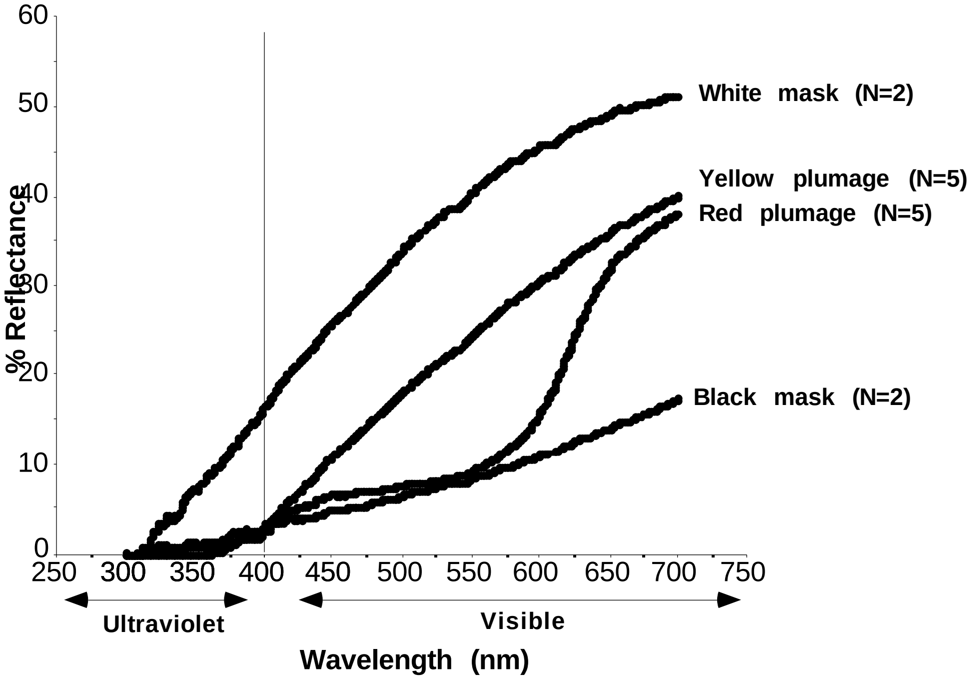

Figure 3.2.. % Reflectance in the UV-visual spectrum as a function of wavelength in 5 specimens of red-billed queleas from Zimbabwe. Reflectance spectra were taken at the center of the breast, crown and throat for each male. Note that no part of a male's plumage reflected peaks in the ultraviolet spectrum.

Morphological measurements.

For each male of the above sample i also measured the following characteristics:

1) Wing length (flattened) measured with a wingrule (to the nearest 0.2 mm).

2) Upper bill length measured with dial calipers (to the nearest 0.1 mm).

3) Tarsus length measured with dial calipers (to the nearest 0.1 mm).

4) Mass before and after the crop contents were removed, measured with an Ohous portable 100g scale (to the nearest 0.1 g).

5) Right and left testis volume. For an easy and reliable way to measure testis volume, I dissected out the testis, placed it into the back end of a 1cc tuberculin syringe, pushed it down to the front end with the plunger and measured volume (to the nearest 0.01 ml) off the syringe directly ($r_I = 0.99$, $F_{55,54} = 522.7$; $P < 0.0001$, J. Dale, unpublished data.)

6) Tail growth bar length. Tail growth bars (ptilochronology) are bands that are subtly visible along the feather, running perpendicular to the shaft. The interval between adjacent bands is thought to correspond to a single day's feather growth during molt. Thus birds with longer growth bars are thought to have been in relatively better condition because they were able to grow their feathers faster when they were molting (Grubb 1989; Hill and Montgomerie 1994; Keyser and Hill 1999). Hill and Montgomerie (1994) and Keyser and Hill (1999) have found strong positive correlations between feather growth bar length and the extent of plumage coloration in house finches and blue grosbeaks respectively. Tail growth bar length was measured here as the mean length of 7 alternating light and dark bands centered around

the point 60% up the length of the bird's right second outermost rectrice (Hill and Montgomerie 1994).

7) Percent insects in the crop. The vast majority of a quelea's diet is seeds; however during breeding they feed much more heavily on insects (Ward 1965). In particular, parents feed their offspring a large amount of insects. Males of differing degrees of quality may vary in their abilities to catch and collect insects for their young (see below). For an easy measure of insect capture, I removed the crop contents and separated out the insect matter from the seed matter. I flattened both piles to a uniform height (1mm) and circular shape. I measured the diameter of the circles and used their relative areas to estimate percent of total crop content

Indices of Phenotypic Quality

I used the above measurements to obtain 10 separate measures of quality, all of which are arguably associated with overall phenotypic constitution. These measures are 1) body mass, and 2) the residuals of body mass regressed onto tarsus length (hereafter "residual mass"), as measures of overall body size and phenotypic condition. 3) wing length as a measure of overall size a male was able to attain during his last molt. 4) tarsus length and 5) bill length as measures of overall skeletal body size. 6) Combined testis volume as a measure of the ability to invest into reproductive tissue growth and/or withstand the costs of larger testes (such as higher testosterone levels, for example). 7) Growth bar length, as a measure of nutritional condition at the time of molt. And finally, 8) the mass of food in the crop, 9) the % insects in the crop and 10) the total mass of insects in the crop (calculated as % insects in crop multiplied by total crop mass), as measures of food-obtaining abilities. For the latter three measures, I restricted the analysis to birds that had 0.5 g or more of food in their crops at the time of capture. My reasoning for this was that all males in the sample were mist netted within a colony on a day they had 5 day old chicks in their nests: a time when paternal feeding trips are at a peak. Therefore most males caught were presumably either heading towards their nests with food to feed young (food in crops), or leaving their nests after a recent feeding trip (empty crops). The bimodal distribution present in crop mass for the entire sample supports this assumption (Figure 3.3).

Replicate sample.

For some analyses, I was able to perform a replicate analysis on a separate sample of 524 males that had been caught at the same colony, but on different days (13 and 15 Mar, 1995; 3-5 days earlier in the breeding cycle than the main sample). These males were kept in deep freeze for 6 weeks before being processed. Due to time constraints, I limited my measurements in this sample to only plumage hue, mask shade, wing length, tarsus length and bill length.

Note on the statistical analysis.

I use correlational analysis throughout most of this paper. Since I have measured a large number of features, it would be appropriate to use a Bonferoni adjustment on most of the results reported here. However, since

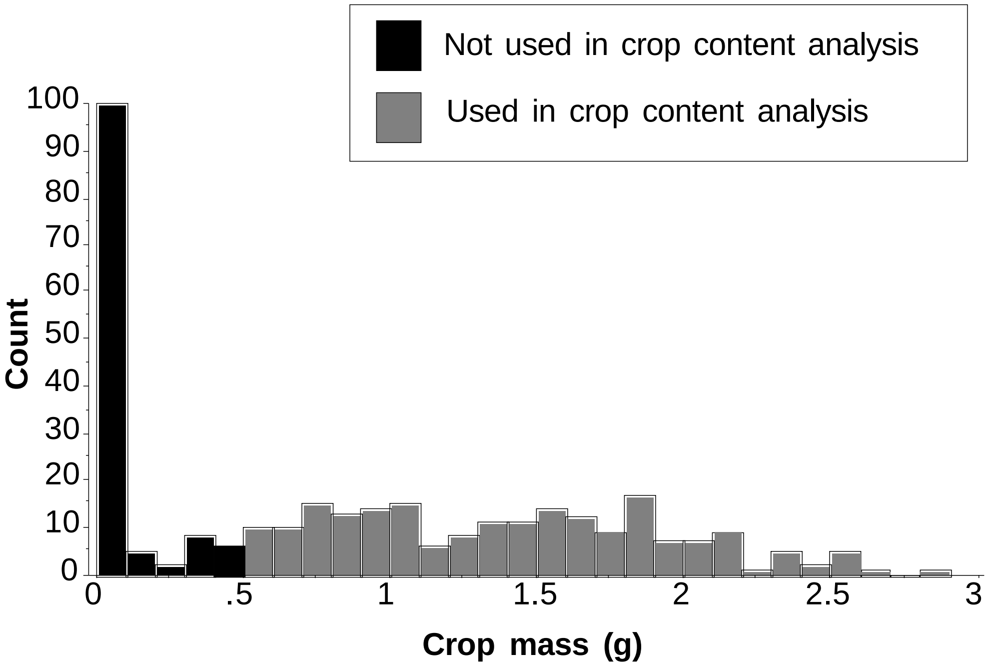

Figure 3.3. Distribution of crop content weights in 324 male red-billed queleas caught at a breeding colony that was in the nestling-feeding stage of the breeding cycle (nestlings were approximately 5 days old). Only males with 0.5 g of food or more were included in further analysis of crop contents.

my thesis in this paper is that plumage traits in red-billed queleas are not significant predictors of quality, then the more conservative approach is to *not* use the Bonferoni method. The reader should keep in mind, therefore, that most of the few significant correlations reported in this paper would be rendered insignificant by a Bonferoni adjustment.

Results

Plumage distributions

The plumage characters showed dramatically high, continuous variation (Figure 3.4). Crown and breast hue varied from red to yellow, breast saturation varied from pale to rich, breast brightness varied from rather dark coloration to very bright, patch area varied from small-sized patches centered on the upper breast, to very large patches covering the entire bird's breast and lower belly, mask shade varied from jet black to bright white, and mask length varied from a tiny patch of black on the eyebrows to a thick bar up to 5 mm long. The two plumage hue characters, and mask shade, all had pronounced bimodal distributions (Figures 3.4 a,b & f). Breast saturation, breast brightness and mask length all showed clear central-tendency distributions with no pronounced skew (Figures 3.4 b, c & g). Finally, patch area displayed a central tendency distribution, although it was skewed considerably to the left (Figure 3.4 e) because a relatively small percentage of males had pigmentation present on their bellies. Of those males, some had slightly different hues on their belly pigmentation than they had on their breast or had a visible gap between the chest and the belly, suggesting that belly coloration is possibly a bimodal trait that is "on/off" as opposed to being a continuously increasing singular patch area.

The frequency distributions reported here provide quantitative support for Ward (1966) who established what has become the traditional color categorization scheme for queleas. Ward distinguished "buff" colored males from males with a "pink suffusion"; and a "white-faced" morph from a "black-faced" morph. These categorizations correspond closely with the bimodality present in the breast/crown hue and mask-shade measurements reported here. However it is important to stress, as Ward (1966) did, that plumage color in queleas varies in a clearly continuous pattern, and so there is inevitably some difficulty classifying intermediate birds as belonging to one "morph" or the other. For example, with mask shade there are a great many black-faced males, and a smaller number of white-faced males. However, males with brown, tan, buff and cream colored masks also occur with regular, albeit low, frequency. Similarly with breast hue, males occur with distinctly red, orange, pink, brown, yellow and buff colored plumage.

Other plumage characters (not quantified) also contributed to a remarkable degree of plumage variability in queleas. For example, further variation arose from highly variable "chin lengths" (the distance the facial mask extends downward from the base of the lower bill), the presence/absence of reddish eyebrow streaks within yellow crowned males, the presence/absence of black ear tufts within white-masked males, and the presence/absence of black foreheads within brown-masked birds.

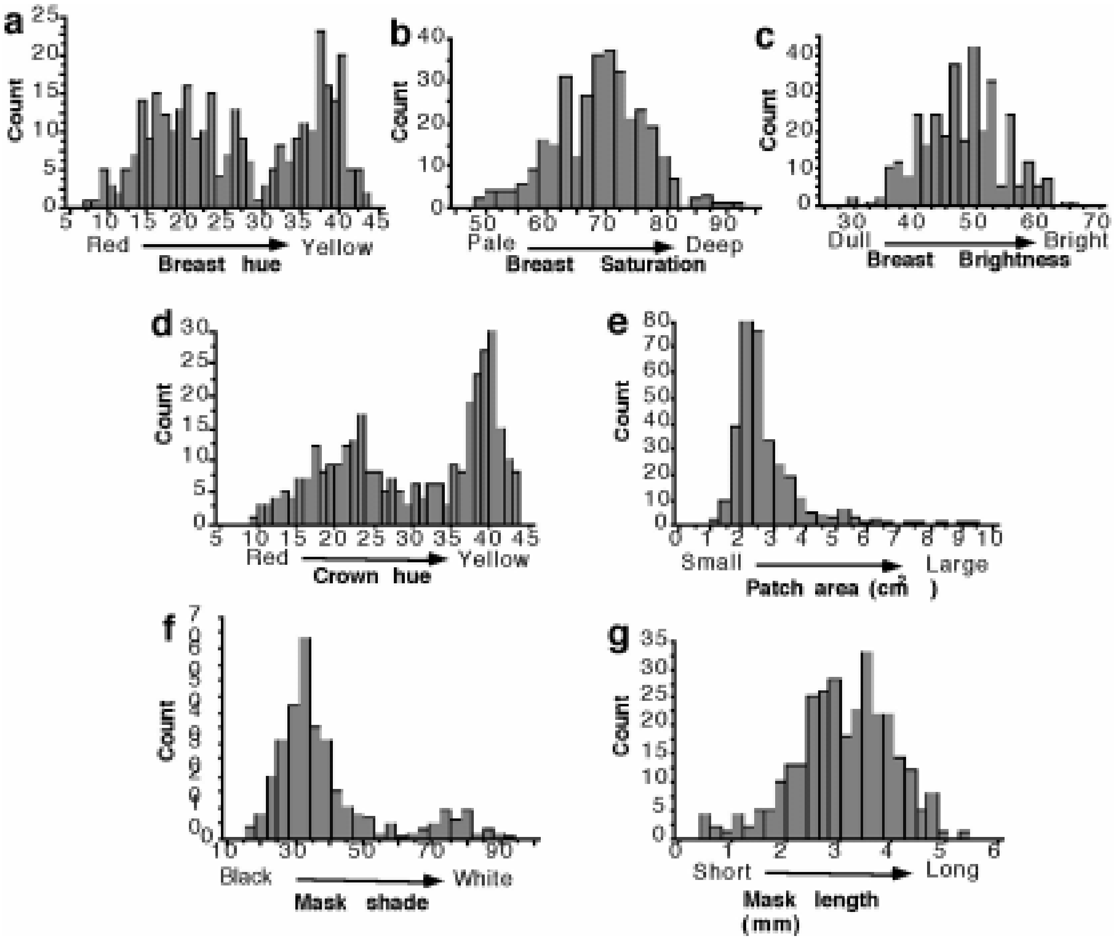

Figure 3.4. Frequency distributions of seven variable plumage characters occurring in breeding male red-billed queleas (N = 324).

Intercorrelations

Since there was a broad range of phenotypes present for all of the characters measured in this study, the resultant amount of color variation was extremely high. The overall variation in plumage color was compounded even higher still because many of these characters co-varied independently of one another (Table 3.1). Indeed, close examination of Table 3.1 reveals a particularly striking pattern: four of the plumage characters, breast hue, patch size, mask length and mask shade, all varied entirely independently of each other. The combination of these four traits together provide a vast supply of total variation. For example, if each of these four plumage traits were considered to only have two states (e.g. red vs. yellow for breast hue, and large vs. small for patch size) then in combination there would be a total of sixteen distinct plumage varieties. Since each plumage trait is in actuality a continuous and broad spread of states, then (depending on this species' discriminatory abilities) the number of distinctive plumage types in queleas is really much higher than that.

A major exception to the general observation of low correlations between plumage characters is the result that breast hue, saturation and brightness were all very strongly correlated with each other. This is not a surprising result because these three characters represent aspects of what can presumably be considered a single and highly variable trait: "breast *color*" (i.e. these traits are likely assessed together by receivers as a "gestalt"). Furthermore, breast hue was very strongly and positively correlated with

Table 3.1. Correlations between plumage characters in male red-billed queleas. Mask Length was measured only in birds with black to light brown masks, as there is no measurable mask length in many white-masked males.

	Breast Sat	Breast Bri	Crown Hue	Patch area	Mask shade	Mask length
Breast hue	$r_S = 0.48$ **$P < 0.0001$**	$r_S = 0.53$ **$P < 0.0001$**	$r_S = 0.85$ **$P < 0.0001$**	$r_S = 0.04$ $P = 0.49$	$r_S = -0.03$ $P = 0.62$	$r_S = -0.05$ $P = 0.44$
Breast Sat	-	$r_S = -0.59$ **$P < 0.0001$**	$r_S = -0.35$ **$P < 0.0001$**	$r_S = 0.07$ $P = 0.21$	$r_S = -0.06$ $P = 0.26$	$r_S = 0.10$ $P = 0.10$
Breast Bri	-	-	$r_S = 0.44$ **$P < 0.0001$**	$r_S = 0.17$ **$P = 0.002$**	$r_S = 0.13$ **$P = 0.024$**	$r_S = -0.09$ $P = 0.14$
Crown hue	-	-	-	$r_S = 0.01$ $P = 0.88$	$r_S = -0.02$ $P = 0.78$	$r_S = -0.03$ $P = 0.65$
Patch area	-	-	-	-	$r_S = -0.03$ $P = 0.65$	$r_S = -0.09$ $P = 0.15$
Mask shade	-	-	-	-	-	$r_S = -0.04$ $P = 0.55$

crown hue (Ward 1966). This result is also perhaps unsurprising if overall plumage hue is coded for at the same set of loci. Finally, it is noteworthy that breast brightness was significantly correlated with both patch size and mask shade. Males with less dark/more bright breast plumage tended to have larger breast patches and whiter face-masks. This suggests that a small amount of the variation in these three characters may be influenced by a common, unknown, factor. For example, a possible mechanism may be that males with particularly dark masks might also tend to deposit more melanin into their breast plumage which would a) make the overall breast plumage darker (less bright) and b) render the outer edges of the carotenoid patch less distinct (giving it an overall smaller appearance).

A closer examination of the correlation between breast hue and crown hue revealed an interesting pattern. About 15% of birds with red breast plumage had yellow crowns, while all but one of the birds with yellow breast plumage had yellow crowns (Figure 3.5; also see plate1, lower left specimen). Individuals with red breasts and yellow crowns maintain these patterns over successive breeding seasons (J. Dale, unpublished data) suggesting a genetic basis to the red-breast/yellow crown variety. That only yellow crowns appear with red breasts, and not vice-versa, is presumably a product of the underlying genetic mechanisms controlling the phenotype (for example, a modifier allele that limits the expression of red-pigment to the ventral area only). Nevertheless, whatever the mechanism, the result is a further increase in the overall variability of the males.

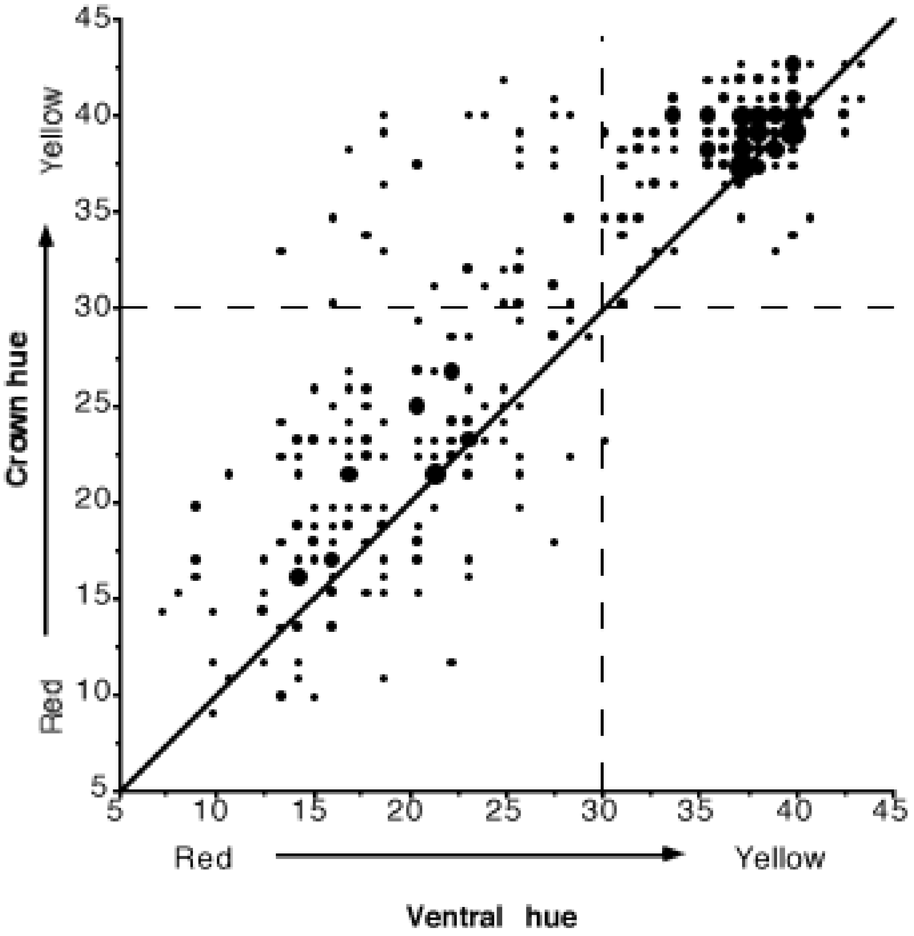

Figure 3.5. Scattergram of crown hue vs. breast hue in breeding plumage of male red-billed queleas (N=324). The horizontal and vertical lines represent approximate cut-offs between red and yellow morphs based on the bimodal distributions evident in Figure 3.4 a & d.

Correlations with indices of quality

Overall, there was very little indication that plumage color was correlated with the different indices of quality used in this study (Table 3.2). I compared all seven plumage measures to a total of 10 different quality indices, for a total of 70 correlations. Six of these 70 correlations were statistically significant. With regards to size and condition measures, males with redder crowns had higher mass than males with yellower crowns and males with larger plumage patches tended to have smaller tarsi. With regards to indices of food-finding ability, males with more white face-masks tended to have a lower percentage and a lower total mass of insects in their crops. Finally males with brighter breast plumage tended to have lower crop masses but higher percentages of insects in their crops. Curiously these two factors cancelled each other out, resulting in no significant correlation between plumage brightness and total amount of insects in the crop.

By chance alone there should be about three or four significant correlations in this sample (at alpha=0.05), so it may be that the six significant correlations described above were spurious and not biologically meaningful. It is important to stress that while some of these correlations are statistically significant, the overall result is that there is no clear pattern. For example, if one considers only "residual mass", which is the most generally used index of phenotypic condition in birds (indeed it is often referred to simply as "condition'), then this conclusion is quite clear: all the different plumage coloration characters in queleas do not appear to be condition-dependent.

Table 3.2. Spearman rank correlations between plumage colouration and 11 measures of phenotypic quality in male red-billed queleas all trapped from the same colony.

	Breast hue	Breast Saturation	Breast Brightness	Crown hue	Patch area	Mask shade	Mask length
Mass (N=324)	r_S = -0.10 P = 0.073	r_S = -0.06 P = 0.25	r_S = -0.05 P = 0.34	r_S = -0.11 **P = 0.047**	r_S = -0.01 P = 0.79	r_S = 0.03 P = 0.63	r_S = 0.02 P = 0.74
Residual mass (N=320)	r_S = -0.08 P = 0.15	r_S = -0.07 P = 0.21	r_S = -0.04 P = 0.43	r_S = -0.08 P = 0.16	r_S = 0.02 P = 0.71	r_S = 0.03 P = 0.55	r_S = -0.01 P = 0.81
Wing length (N=324)	r_S = -0.02 P = 0.69	r_S = -0.02 P = 0.71	r_S = -0.00 P = 0.96	r_S = -0.02 P = 0.74	r_S = 0.01 P = 0.91	r_S = -0.02 P = 0.72	r_S = -0.06 P = 0.31
Tarsus length (N=320)	r_S = -0.09 P = 0.09	r_S = 0.02 P = 0.73	r_S = -0.05 P = 0.35	r_S = -0.10 P = 0.09	r_S = -0.16 **P = 0.005**	r_S = 0.01 P = 0.83	r_S = 0.09 P = 0.11
Bill length (N=324)	r_S = -0.07 P = 0.20	r_S = 0.04 P = 0.53	r_S = -0.02 P = 0.69	r_S = -0.07 P = 0.19	r_S = 0.09 P = 0.09	r_S = -0.02 P = 0.78	r_S = -0.07 P = 0.22
Combined testis Volume (N=283)	r_S = -0.08 P = 0.21	r_S = -0.09 P = 0.14	r_S = 0.03 P = 0.56	r_S = -0.09 P = 0.14	r_S = 0.07 P = 0.25	r_S = -0.08 P = 0.17	r_S = -0.04 P = 0.56

Table 3.2. (Continued)

	Breast hue	Breast Saturation	Breast Brightness	Crown hue	Patch area	Mask shade	Mask length
Growth bar length (N=128)	r_S = -0.02 P = 0.79	r_S = -0.08 P = 0.36	r_S = -0.02 P = 0.86	r_S = -0.07 P = 0.41	r_S = 0.002 P = 0.98	r_S = -0.11 P = 0.23	r_S = -0.07 P = 0.44
Crop mass (N=203)	r_S = 0.01 P = 0.90	r_S = -0.17 **P = 0.016**	r_S = -0.09 P = 0.20	r_S = 0.02 P = 0.74	r_S = -0.10 P = 0.15	r_S = -0.01 P = 0.86	r_S = -0.09 P = 0.25
% Insects in crop (N=203)	r_S = -0.003 P = 0.97	r_S = 0.15 **P = 0.032**	r_S = -0.004 P = 0.96	r_S = 0.003 P = 0.96	r_S = -0.05 P = 0.45	r_S = -0.15 **P = 0.032**	r_S = 0.05 P = 0.51
Insect mass in crop (N=203)	r_S = 0.007 P = 0.92	r_S = 0.09 P = 0.18	r_S = -0.01 P = 0.86	r_S = 0.02 P = 0.74	r_S = -0.08 P = 0.24	r_S = -0.15 **P = 0.034**	r_S = 0.02 P = 0.81

Finally, a separate analysis on the second replicate sample of males confirmed that there were no significant correlations between overall body size (wing, tarsus and bill size) and breast hue or mask shade (Table 3.3). This analysis demonstrated that at least one of the correlations observed in the first sample was indeed spurious (tarsus length vs. patch size; the other correlations were not replicated in the second sample).

Correlations with quality within different plumage "morphs"

Since mask shade and breast hue have bimodal distributions, it is possible that plumage color is related to condition within broader color classes. For example, even though over the entire sample, plumage hue is not correlated to condition, it is still possible that within the group of birds with reddish plumage there might be a correlation between how red a male is and his condition. In other words, deep red males might be in better condition than less red males, and deep yellow males might be in better condition than less yellow males. To evaluate these possibilities, I separated birds into broad plumage classes and then evaluated the differences in condition between classes using F-tests. For breast hue, males were divided into five categories: deep red, red, intermediate, yellow and deep yellow (Figure 3.6 a). For mask shade, males were divided into four categories: black, brown, intermediate, and white (Figure 3.6 b). The results of these analyses, using both samples of birds and presented in Tables 3.4 (breast hue) and 3.5 (mask shade), demonstrate that there were no complex relationships between plumage

Table 3.3. Spearman rank correlations between plumage coloration and 3 measures of size in male red-billed queleas all trapped from the same colony (13 and 15 Mar 1995).

	Breast hue	Mask shade
Wing length	$r_S = -0.003$	$r_S = 0.06$
(N=544)	P = 0.95	P = 0.13
Tarsus length	$r_S = 0.08$	$r_S = -0.04$
(N=540)	P = 0.07	P = 0.40
Bill length	$r_S = 0.03$	$r_S = 0.01$
(N=546)	P = 0.43	P = 0.76

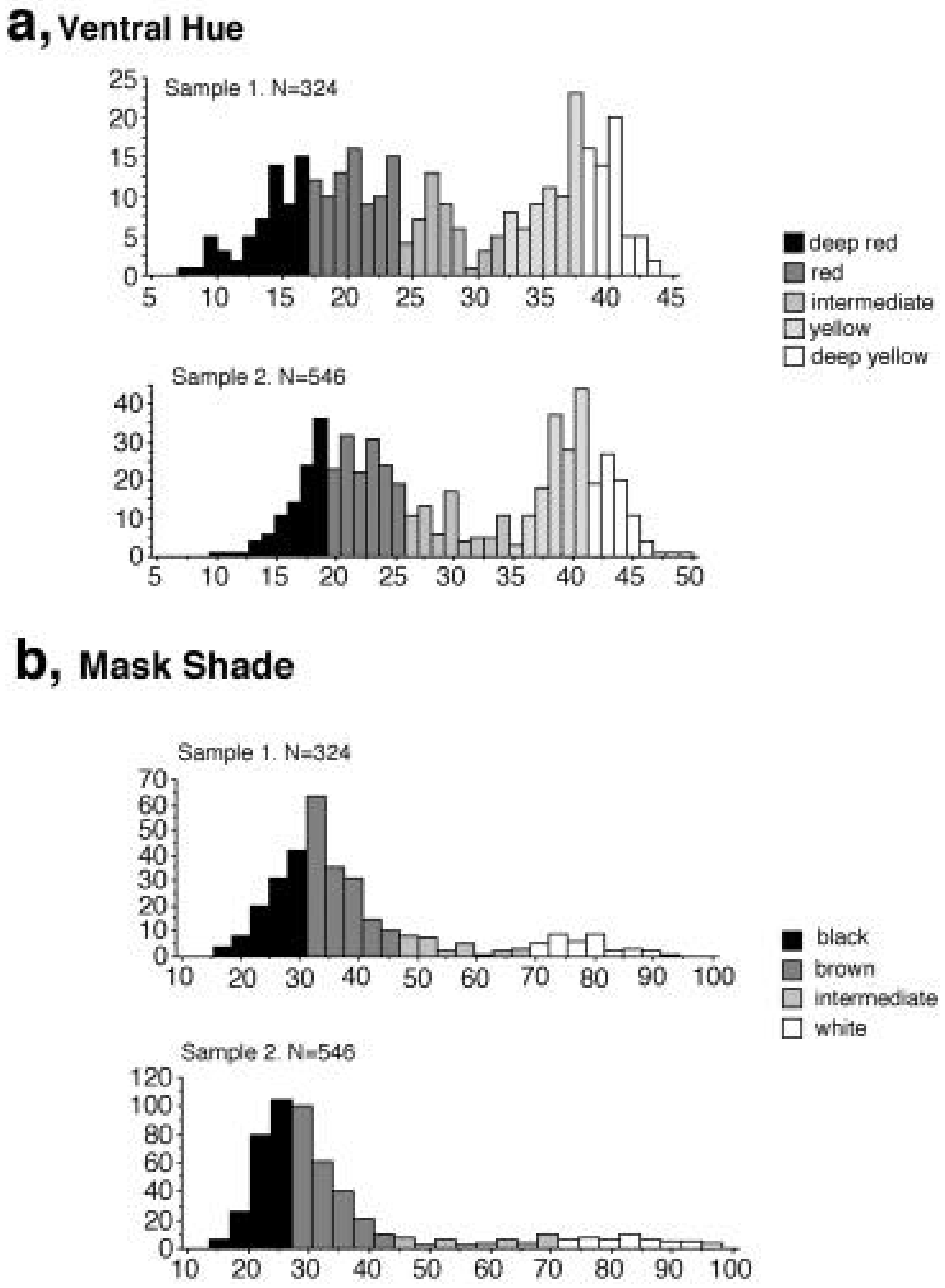

Figure 3.6. Distributions of ventral hue and mask shade in two replicate samples of male red-billed queleas. In an analysis designed to detect non-linear correlations between plumage color and condition, males were divided into categorical groups on the basis of these distributions.

Table 3.4. Means ± s.d. for condition and size measures in red-billed queleas divided into broad colour groups based on the hue of their breast plumage

	Red	Dull red	Intermediate	Dull yellow	Yellow	F-test	P
SAMPLE 1	N=62	N=85	N=62	N=69	N=46		
Mass (g)	19.46±1.05	19.14±1.10	19.05±1.24	18.97±1.13	19.24±1.14	1.78	0.13
Residual mass (g)	0.16±0.96	0.02±1.06	-0.07±1.15	-0.15±1.10	0.06±1.08	0.82	0.52
Wing length (mm)	67.07± 1.25	66.83±1.15	66.85±1.17	66.80±1.13	66.93±1.13	0.58	0.67
Tarsus length (mm)	21.07±0.50	20.84±0.54	20.83±0.58	20.81±0.52	20.90±0.53	2.57	**0.038**
Bill length (mm)	14.05±0.40	14.04±0.38	14.02±0.35	14.0±0.33	14.1±0.30	0.72	0.58
Testes Volume (ml)	0.257±0.047	0.247±0.054	0.257±0.06	0.238±0.050	0.253±0.064	1.16	0.33
Growth bar (mm)	2.74 ± 0.16	2.74 ±0.18	2.73 ±0.17	2.75 ± 0.18	2.66 ±.18	0.40	0.81
Crop mass (g)	1.36 ± 0.51	1.38 ±0.61	1.22 ±0.55	1.35 ± 0.55	1.43 ±.52	0.83	0.51
% insects in crop	0.22 ± 0.22	0.21 ±0.28	0.22 ±0.26	0.26 ± 0.24	0.21 ±.26	0.24	0.92
Insect mass	0.30 ± 0.33	0.26 ±0.33	0.28 ±0.36	0.33 ± 0.32	0.27 ± 0.34	0.24	0.91

Table 3.4. (continued)

	Red	Dull red	Intermediate	Dull yellow	Yellow	F-test	P
SAMPLE 2	N=113	N=121	N=93	N=119	N=100		
Wing length (mm)	66.67±1.27	66.92±1.05	66.56±1.24	66.75±1.21	66.73±1.14	1.34	0.25
Tarsus length (mm)	20.69±0.51	20.68±0.58	20.62±0.64	20.73±0.57	20.81±0.65	1.32	0.26
Bill length (mm)	14.06±0.31	14.02±0.37	14.06±0.39	14.10±0.30	14.08±0.39	0.94	0.44

Table 3.5. Means ± s.d. for condition and size measures in red-billed queleas divided into broad colour groups based on the shade of their mask

	Black	Brown	Intermediate	White	F-test	P
SAMPLE 1	N=62	N=85	N=62	N=69		
Mass (g)	19.07±1.12	19.26±1.12	19.05±1.16	19.22±1.28	0.77	0.51
Residual mass (g)	-0.08±1.03	0.09±1.07	-0.14±1.08	0.08±1.22	0.76	0.52
Wing length (mm)	66.93±1.25	66.90±1.08	66.75±1.01	66.86±1.42	0.22	0.88
Tarsus length (mm)	20.85±0.60	20.92±0.51	20.93±0.52	20.82±0.49	0.59	0.62
Bill length (mm)	14.03±0.37	14.02±0.34	13.95±0.35	14.09±0.38	0.91	0.44
Testes Volume (ml)	0.254±0.058	0.250±0.055	0.241±0.50	0.245±0.051	0.53	0.66
Growth bar (mm)	2.72 ± 0.18	2.75 ±0.18	2.70 ±0.20	2.77 ± 0.11	0.57	0.64
Crop mass (g)	1.35 ± 0.55	1.34 ±0.57	1.37 ±0.60	1.35 ± 0.47	0.02	0.99
% insects in crop	0.26 ± 0.27	0.21 ±0.25	0.20 ±0.23	0.16 ± 0.24	1.30	0.27
Insect mass (g)	0.33 ± 0.35	0.27 ±0.32	0.27 ±0.33	0.19 ± 0.29	1.25	0.29

Table 3.5. (Continued)

	Black	Brown	Intermediate	White	F-test	P
SAMPLE 2	N=113	N=121	N=93	N=119		
Wing length (mm)	66.75±1.17	66.69±1.20	66.75±1.06	66.87±1.23	0.34	0.80
Tarsus length (mm)	20.72±0.57	20.72±0.61	20.71±0.55	20.62±0.57	0.40	0.75
Bill length (mm)	14.07±0.34	14.07±0.37	14.07±0.29	14.08±0.36	0.01	0.99

coloration and the quality measures. The one significant result of this analysis, which demonstrated that tarsus size was larger in deep red males, was not confirmed in the second (larger) sample, and so is probably a spurious result.

The above analysis tested only whether breast hue and mask shade were important predictors of quality within different color classes. However, it still may be true that the other plumage traits, such as breast saturation or patch area, could predict condition within different color varieties. In order to evaluate this I tested whether there were any significant correlations between any of the plumage characters and any of the quality indices separately within the four basic plumage "morphs" commonly used to describe quelea plumage (Ward 1966). Table 3.6 lists the correlation coefficients (r) between all the different combinations of traits vs. indices of quality for each of the four plumage "morphs". In this table I have also reported the analogous results for bill hue (Chapter 2; Dale, unpublished data) in order to provide a contrast to the plumage color correlations. Males with redder bills were found to be more dominant (Shawcross and Slater 1983), and to have higher residual mass and longer bill lengths (Chapter 2) than males with yellower colored bills. Therefore bill color is likely a condition-dependent indicator of quality in this species.

For the plumage characters, the basic conclusion that can be drawn from Table 3.6 is that none of the plumage traits are very good at predicting quality when males are compared only within their specific morph types. There were a total of 270 correlations in this table (plumage traits only) and so there should have been about 13 or 14 significant correlations by chance

Table 3.6. Matrix of R-values for correlations between plumage characters and condition indices within different plumage "morphs": R = red hued males; Y = yellow hued males; B = black-masked males; W = white-masked males. Males were classified by eye into either "red" or "yellow" morphs for plumage hue; and as either "white-face" or "black-face" for mask shade. These colour groupings correspond strongly to the bimodal distributions evident in Figure 4 (mean breast hue of birds classified as red = 20.3 ± 6.1 s.d. (*n* = 203), as yellow = 37.4 ± 2.82 s.d. (*n* = 121); mean mask shade of birds classified as black = 33.9 ± 8.6 s.d. (*n* = 282), as white = 76.1 ± 7.66 s.d. (*n* =42)). R-values for bill hue correlations are provided as a contrast to plumage traits (Dale, unpublished data). Significant correlations (P<0.05) are in bold. Significant correlations in the direction opposite to predictions are in parentheses (see text).

Character	Group	Mass	Residua Mass	Wing Length	Tarsus Length	Bill Length	Testes Volume	Growth Bar Len.	Crop Mass	% insect in crop	Insect Mass
Breast Hue	R	-.07	-.03	-.07	-.12	-.06	.00	-.05	.007	.06	.09
	Y	.06	.05	-.04	.07	-.004	-.04	-.04	**(.30)**	.06	.17
	B	-.08	-.06	-.06	-.09	-.10	-.01	.00	.01	.04	.04
	W	-.27	-.24	.13	-.13	.09	**-.38**	-.12	-.09	**-.38**	**-.37**
Breast Saturation	R	.00	-.01	.08	.03	.10	-.14	-.15	-.07	.09	.08
	Y	**(-.22)**	-.24	-.13	.03	-.10	-.08	.02	**(-.35)**	.09	-.07
	B	-.05	-.07	.01	.06	.05	-.11	-.13	**(-.15)**	.12	.08
	W	-.01	-.01	-.04	-.03	.01	.03	.17	-.23	-.04	-.12
Breast Brightness	R	-.06	-.04	-.09	-.07	.00	.12	.02	**(-.20)**	.10	.01
	Y	.06	.07	.14	.02	.08	.01	-.09	.17	-.10	-.02
	B	-.02	-.006	.006	-.06	.00	.08	.01	-.12	.00	-.06
	W	-.28	-.25	-10	-.11	-.07	-.13	-.22	.09	.15	.16
Crown Hue	R	-.06	.01	-.02	-.13	-.08	-.05	-.16	.06	.07	.14
	Y	.02	-.02	.002	.13	.15	-.03	-.09	.13	-.04	.03
	B	-.08	-.05	-.03	-.10	-.08	-.02	-.08	.03	.07	.10
	W	-.29	-.23	.10	-.19	-.01	**-.47**	-.03	-.09	**-.49**	**-.43**

.6. (Continued)

Character	Group	Mass	Residua Mass	Wing Length	Tarsus Length	Bill Length	Testes Volume	Growth Bar Len.	Crop Mass	% insect in crop	Insect Mass
Mask Length	R	.03	.00	-.06	.09	-.03	.01	-.15	**(-.20)**	.04	-.01
	Y	.09	.05	-.09	.12	-.06	-.07	-.03	.21	-.02	.04
	B	.05	.02	-.07	.10	-.04	-.01	-.10	-.06	.02	.01
	W	-	-	-	-	-	-	-	-	-	-
Bill Hue	R	-.12	**-.15**	**-.18**	.03	-.11	-.05	.08	-.03	.04	.08
	Y	**-.20**	**-.20**	-.01	-.03	-.13	-.10	-.07	-.09	-.15	-.17
	B	**-.15**	**-.17**	**-.13**	.02	**-.13**	-.03	.08	-.08	.01	.02
	W	-.23	-.22	-.05	-.10	-.14	**-.38**	-.32	.15	-.19	-.11

R
Y
B
W

alone. In actuality there were 16 significant correlations, and 7 of these occurred in the direction opposite to predictions based on the indicator hypothesis (for example, more saturated males should be higher quality than less saturated males). In contrast, there were 9 significant correlations out of a total of 40 between bill hue and the different quality indices (there should have been about 2 significant correlations by chance alone); and all of them were in the direction predicted by the dominance study cited above (Shawcross and Slater 1983). Bill hue was best at predicting residual mass (which is the standard measure of phenotypic condition) within the different morph types. In contrast, all of the plumage traits were very poor predictors of residual mass.

Discussion

The overall variation in plumage color in red-billed queleas is extreme relative to that observed in most other species of birds. Since quelea plumage is conspicuous, continuous, sexually dimorphic, and occurs only during the breeding season, it is reasonable to expect that plumage coloration in this species is a condition dependent indicator of phenotypic quality. However, the results presented here do not support this hypothesis.

First, quality indicators should generally have unimodal frequency distributions.. These are the frequency distributions that have been observed in the indicator signals of many other species, and they presumably arise from unimodal distributions in the quality underlying the signal (Chapter 5). Why is quality predicted to be unimodal? This prediction assumes that an individual's quality is basically a numerical trait that results from the sum effects of a potentially great number of environmental and genetic factors. These factors will influence and give rise to an individual's overall ability to be successful. It follows that the quantitative outcome of these effects summed across a large sample of individuals will be a unimodal distribution in overall quality within a population.

In queleas, however, three of the seven plumage traits analyzed demonstrated distinct *bimodal* distributions. This observation, taken on its own, does not absolutely refute the hypothesis that quelea plumage is an indicator. However if a trait *is* an indicator signal, and it *is* bimodally distributed, then an explanation of the bimodality would be required. In other words, bimodally distributed indicators are unusual.

Second, there should be positive and significant correlations between the separate component traits of an animal's indicator signals (Kodric Brown and Brown 1984). This prediction assumes that the different indicators reflect, at least in part, overlapping aspects of quality. Although it can be argued that different indicators can theoretically be signaling different information, they should still be positively correlated if they are each condition-dependent. For example, if one trait is an indicator of overall parasite load, and a second trait is an indicator of dominance; then, with large enough samples, a positive correlation should be observed between the two traits. This is because birds with high parasite loads will, in general, tend to be better fighters. This is essentially true for all the different information that indicators are thought to potentially reveal: fighting ability, dominance, nutritional condition, age, parasite loads, good genes, survivability, glucose levels, etc are all going to tend to be positively correlated with each other. Indeed, positive correlations have been observed between separate component traits in the indicator signals of many species (e.g. plumage hue and patch size in house finches: Hill 1992; tail length and throat hue in barn swallows: Camplani et al. 1999), including indicators that signal in different mediums (e.g. song repertoires and plumage color in pied flycatchers (Lampe and Espmark, 1994)) . Lack of a correlation therefore can be taking as evidence that at least one of the traits is not an indicator of quality.

In queleas, however, the different plumage characters analyzed here are characterized by a pronounced lack of significant correlations with each other.

Third, and most importantly, condition dependent indicators should be correlated with measurable indices of phenotypic quality (Andersson 1994). High quality males should be better able to afford the theoretically required costs that keep indicator signals honest. Indeed, many of the indices of quality I used in this study have been commonly used in other studies and have been found to correlate significantly with secondary sexual ornaments in many other species (Table 3.7).

In queleas however, the seven different plumage traits were not related in any predictable way with any of ten measures of quality. This was true even when I analyzed groups of different color varieties separately.

In order to obtain perspective on how different the patterns of plumage coloration in queleas appear to be in comparison to many other species hitherto studied, I compared the overall results reported here to

Table 3.7. Comparison of patterns of frequency distributions, intercorrelations, and condition-dependence in plumage traits of red-billed queleas vs. other species whose plumage traits are believed to signal quality. N/A indicates no relevent data.

	Queleas	House Finches 1,2	House Sparrows 3,4	Barn Swallows 5	Pied Flycatchers 6,7	Auklets 8	Widowbirds 9,10	Cardinals 11
Frequency Distributions	Bimodal & Unimodal	Unimodal	Unimodal	Unimodal	Unimodal	Unimodal	Unimodal	Unimodal
Significant Intercorrelations	No	Yes	n/a	Yes	Yes	n/a	n/a	n/a
Condition Dependent?	None	Residual mass Size Ptilochronology	Mass Testes size	Size Testes size	Size	Residual mass	Residual Mass Wing size	n/a

References. 1) Hill pers. comm.; 2) Hill & Montgomerie 1994; 3) Møller & Eritzoe1988; 4) Møller 1989, 5) Møller 1994; 6) Jarvi et al 1987, 7) Dale et al 1999, 8) Jones and Montgomerie 1992; 9) Alatalo et al. 1988; 10) Andersson 1992; 11) Wolfenbarger 1999a.

analogous patterns observed in seven different species, the plumage of all of which are argued to be indicators (Table 3.7). Overall, the patterns described here for red-billed queleas contrast strongly with patterns observed in the ornamental plumage of other species.

Four additional pieces of evidence argue against quelea plumage being a quality indicator. First, queleas held in captivity and maintained on a basic diet of seed only, demonstrated the full spectrum of plumage color as seen in populations of wild birds, indicating that quelea plumage does not have a strong degree of environmental determination. Second, individual males molted into identical plumages over successive breeding seasons, indicating that plumage coloration is a fixed trait that does not change with age. Third, captive raised offspring molted into breeding plumages that were similar to those of their wild fathers, indicating that quelea plumage has a high degree of genetic determination, based on the inheritance of alleles at polymorphic loci coding directly for plumage color. And finally, plumage coloration did not correlate with reproductive success in a large sample of males monitored at wild breeding colonies (Chapter 2).

Alternative hypotheses

If quelea plumage is not a quality indicator, then what function does it serve? I outline a number of possibilities below. I suggest that the patterns of plumage coloration in queleas are most consistent with the hypothesis that plumage functions in individual recognition as a signal of individual identity.

Two other hypotheses, neutral mutation and compatible-mate cue, are also possibilities.

Neutral mutation. The null hypothesis is that quelea plumage coloration has no adaptive value. Such a state could arise, for example, from neutral mutations spreading by genetic drift (Ford 1975; Hedrick 1983; Falconer 1989), from by-products of pleiotropy (Møller 1994) , or from neutral mixing of previously isolated subspecies (Cooke et al. 1995). Neutrality is a difficult hypothesis to rule out. However there are at least three lines of evidence suggesting this hypothesis is unlikely.

First, characters that spread by drift are expected to demonstrate extreme geographic variation, with the frequency of alleles drifting to zero and/or 100% across different populations (Hedrick 1983). Similarly, a historical mixing of previously isolated subspecies should demonstrate clear geographical clines with certain alleles being fixed or entirely absent in those populations that occur on the edges of the zone of mixing (as seen in snow geese *Anser caerulescens*, Cooke et al. 1995). A survey of the geographical variation in quelea plumage color demonstrates that indeed there is substantial geographic variation in this species, but that all the different varieties are present at significant proportions in all populations (Figure 3.7). Therefore, the overall intra-population variability is high throughout the entire geographic range (Ward 1966). Indeed, the white-face morph is maintained at relatively low and static levels (5 to 20%) throughout all of sub-

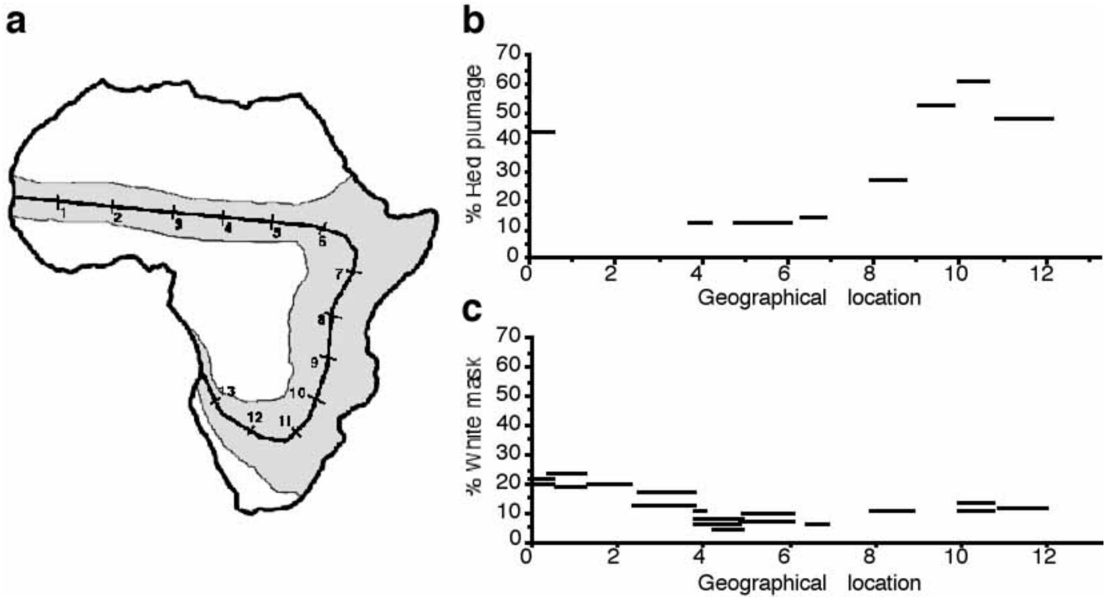

Figure 3.7. Geographical variation in quelea breeding plumage. a) Geographical range of quelea. To quantify geographical variation along a cline I drew a line centrally through the range and used the position along that line to define the position of a population along a linear scale. b) variation in % of males with red plumage. c) variation in % of males with white plumage. Data are from Ward (1966), Manikowski et al. (1990), and J. Dale (unpublished data).

Saharan Africa: a geographical distribution that encompasses three separate subspecies. This observed pattern is more consistent with the idea that the white-faced morph is a balanced polymorphism (Ward 1966), presumably maintained in populations through negativly-frequency dependent selection (see below) as opposed to genetic drift.

Second, Ward's (1966) observation that there is subspecific variation in body size provides further insight into the hypothesis that quelea plumage polymorphism is a neutral by-product of a subspeciation event coupled with a post-subspeciation merger of populations (Cooke et al. 1995). Specifically, East African populations tend to be larger than southern African populations. Since percentages of red males in eastern African populations are lower than in southern populations (Figure 3.7), there is a negative correlation between mean bill size and percentage of males with red plumage color *between* populations (Figure 3.8). If plumage color was correlated to what ancestral subspecies a male belonged to, and one ancestral subspecies was bigger than the other, then you should also find a correlation between size and plumage color *within* populations after the two subspecies have undergone mixing. However within populations there is no relationship between body size and plumage color (this study).

A final argument against neutrality is simply that quelea plumage color is conspicuous, it occurs in males only, it occurs during the breeding season only, and it is displayed on the parts of males that would be most visible to other queleas during interspecific interactions (i.e. the face, breast, and crown). These are the types of traits that should have fitness consequences on their

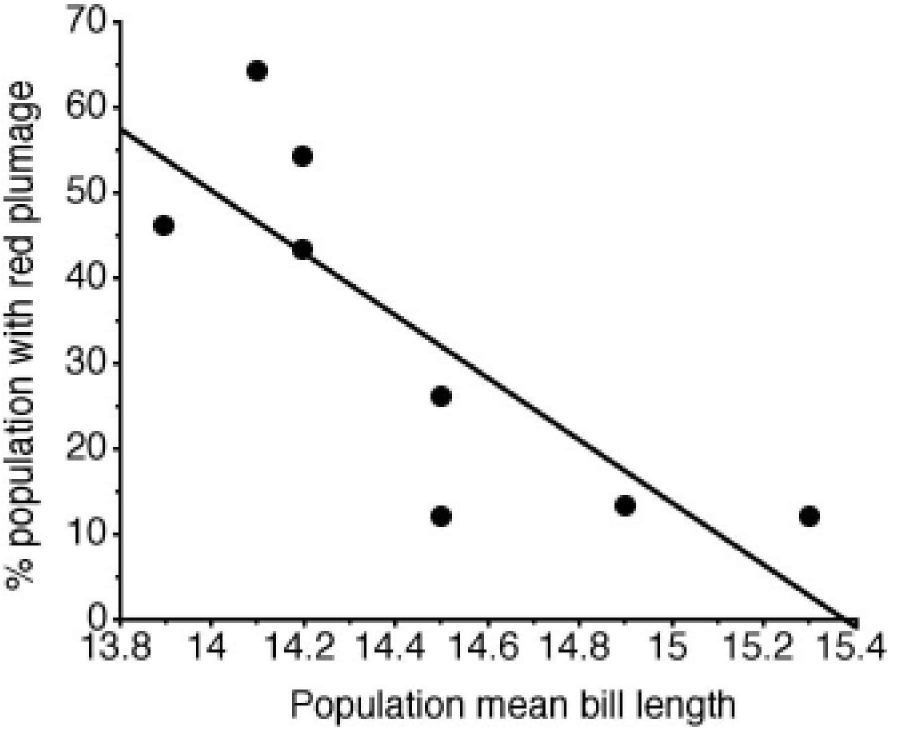

Figure 3.8. % red males vs. mean population bill size across 8 separate populations of red-billed queleas, spanning their entire geographical range. Data are from Ward 1966.

bearers. Thus, the characteristics of the phenotype suggest that it has been designed by selection to be signal.

Fisherian Runaway Trait

Fisherian runaway selection is commonly invoked to explain dramatic cases of sexually-selected ornamentation in animals. Models of runaway sexual selection argue that the genes for the expression of male traits and the genes for the female preferences for those traits become genetically linked through assortative mating. Thereafter, the trait genes and the preference genes can co-evolve into extreme forms as the two character traits amplify each other in a self-reinforcing runaway process (O'Donald 1983). Under this hypothesis, traits are not required to honestly convey information about phenotypic condition. It is unlikely however, that quelea plumage is a Fisherian “runaway” trait because runaway sexual selection is expected to result in *decreased* intra-population variance (Alatalo et al. 1988). In queleas, intra-population variance in plumage coloration is remarkably high. Secondly, runaway traits are typically assumed to be quantitative traits with unimodal distributions (e.g. O' Donald 1983). In queleas, the two most conspicuous features, plumage hue and mask shade, have bimodal distributions.

Differential microhabitat selection

Another explanation for why queleas are so polymorphic is that males could experience fluctuating selection pressures under different microhabitats. For example, certain color classes may be preferentially chosen by females or predated upon differentially, depending on whether they nest high in trees (with the open sky as background) or closer to the ground (with thicker vegetation as background). These types of hypotheses can be eliminated because they predict color "morphs" will be found associating within their favored microhabitats (Hazel and Johnson 1990; Morey 1990). However they do not: color "morphs" were distributed randomly throughout colonies (Chapter 4).

Kin association signal

Kin effects may be of widespread importance in avian social interactions. For example, peacocks were found to preferentially lek with close relatives, even in the absence of social learning or environmental cues (Petrie et al. 1999). Presumably the peacocks were basing their lek-partner choices on some sort of phenotypic variation used to ascertain potential relatedness. In queleas, since plumage variation is genetically determined (Chapter 2), maintenance of selection for plumage variability could occur via benefits obtained through altruism received from genetically related individuals. Similar to the preceding hypothesis, however, Kinship signaling can be ruled out because it predicts spatial clumping of different color "morphs" (Petrie et al. 1999).

Complimentary-mate cue

Plumage color in queleas could function as a signal used by females to determine genetic complimentarity of prospective mates. For example, if females look for males with complementary genes for parasite resistance (Wedekind 1994), then selection may favor signals that reveal a male's resistance type. If different resistance types are maintained by negatively-frequency dependent selection, a polymorphic distribution of signals will be observed among males. Such signals do not require a cost associated with them; and therefore they would not be expected to be condition-dependent. As with the neutral mutation hypothesis, this hypothesis can not be ruled out. However there is reason to believe that it is unlikely.

It is unclear how such a system could remain stable in a sexually-dimorphic signaling system. If certain character states resulted in lower matings for males whose complimentary female resistance types were rare, then those males would be selected to cheat by falsely signaling the more common resistance states. The result would be a breakdown of the correlation between signal state and resistance type. Wedekind (1994) argued that males will only be selected to broadcast their resistance types honestly as long as they profit more by increasing the survival probability of fewer offspring, than they would by trying to have as many offspring as possible. However, under such conditions males should also be selected to be as choosy as females about their mating partners. Therefore such signals should be found in sexually monomorphic characteristics that are used by both sexes during mate assessment. I suspect that such signals will be rare in conspicuous sexually-dimorphic ornaments such as quelea plumage.

Complimentary-mate signaling may explain odor-based mate-choice for cues strongly connected to the major-histocompatibility complex (MHC) of the immune system (Egid and Brown 1989; Wedekind and Füri 1997). Highly variable glycoproteins encoded by polymorphic MHC loci will create detectable odors via 1) a breakdown of the glycoproteins themselves into small evaporating molecules, and / or 2) by determining the specificity of the odor-causing bacterial flora that are able to inhabit an individual (Wedekind 1994). In such a signaling system there is tight mechanism coupling the odor-cues to the resistance genotype because MHC genes also effect susceptibility to different pathogens. Under the assumption that it is impossible (or highly costly) for a male to produce an odor specific to a particular MHC allele unless they actually carry it; then females may be able to *force* males into broadcasting their resistance genotype honestly by choosing mates on the basis of MHC-related odor cues. In contrast, since there is no clear mechanism whereby variance in plumage loci will be coupled to variance in the resistance loci, then in the absence of unforced honesty, plumage characteristics are probably a poor medium for broadcasting genetic resistance type.

Individual Recognition Signal

There are three lines of evidence that suggest that quelea plumage might function as a signal of individual identity that is used in individual recognition (Whitfield 1986; 1987; Beecher 1982; Chapter 5).

First, individual recognition signals (IR signals) should occur in species which have socioecological parameters associated with greater benefits to being recognizable. In quelea colonies, such conditions are arguably very important. Colonies are immense (millions of birds), densely packed, and have high rates of social interactions occurring among potentially huge numbers of individuals. Furthermore, reproductive synchrony is so high that nest building is initiated and completed by males *en masse* over the course of only three days (Crook 1960; Chapter 4). Therefore, males form their nest-territories concurrently with multiple nest-neighbors over a very short time period (females do not participate in nest-building and territorial defense (Crook 1960)). Whitfield (1987) argued that IR signals will be more prevalent in species where stable, but relatively large, groups form. Such conditions certainly occur within neighborhoods of nesting queleas. Furthermore, it is possible that red-billed queleas may actually form cohesive social units, within their immense aggregations, that may persist for 6 months or longer, throughout nesting and migration periods (Jaeger et al. 1986). Males breeding in nest-neighborhoods, and occurring in possibly more long-term social groups, will interact repeatedly with their mates, territorial nest-neighbors and possibly with more long-term social-group members. Since all these social interaction will occur within a background of an immense flock of unfamiliar individuals, then males who have features which increase their recognizability might experience fitness benefits.

Second, an assumption of the identity-signaling hypothesis is that individuals should discriminate familiar individuals from unfamiliar ones via variance in the hypothesized identity signal. That is; the selective benefit to signaling individuality hinges on the ability of receivers of the signal to use the information and make decisions accordingly. Therefore, recognition via the cues present in the signal must be demonstrated, or else the identity-signaling hypothesis can be refuted. Preliminary observational evidence suggests that individual recognition is important in quelea colonies. Since nesting density is so high, the defended areas of neighboring territorial males overlap. Neighboring males recognize each other (Crook 1960; Chapter 4.; but see Shawcross and Slater 1983) and tolerate each other much closer to their nests than unfamiliar birds, who are "fiercely attacked" (Crook 1960). This suggests that disputes between neighboring males can be reduced through accurate neighbor-stranger or "Dear Enemy" recognition (Wilson 1975). Further experimental work is required to demonstrate that this recognition occurs through variation in plumage coloration, although it would seem to be an obvious and reliable cue for neighboring males to use. Indeed, recognition via visual cues would be particularly effective in queleas because neighbors are always in close visual contact. By signaling individuality visually (as opposed to, but not in lieu of, acoustically) males would be able to broadcast their identity constantly while simultaneously pursuing other critical activities such as nest building and courtship.

Third, identity signals should demonstrate specific properties. An efficient way to signal individual identity is to have distinctive cues (i.e. conspicuous traits with high population variance) based on multiple characters that are non-correlated to each other and that are relatively cheap (i.e. not condition dependent) (Beecher 1982; Chapter 5). The patterns of quelea plumage outlined here follow these expected signal properties. Additionally, selection for recognizability is negative-frequency dependent, a form of selection that can readily result in polymorphisms (Maynard-Smith 1982), and that is consistent with the bimodality observed in some of the plumage traits.

To illustrate how identity selection could maintain a plumage polymorphism, consider the mask shade phenotype in queleas. Black face masks are a common features of the plumages of species across a number of different bird families, including weavers. Savalli (1995) suggests that such features should be particularly prevalent in species that forage in bright, open environments (such as queleas) because black immediately around the eyes may reduce glare from the sun, and improve insect hunting ability (Ficken et al. 1971; Burtt 1984). In contrast, white facial masks are rare features of birds. Thus in species with black facial masks, any white-faced mutants might be selected against. However, under conditions where there is a strong benefit associated with looking recognizable, the mutation of having a white-mask could spread. Because there might be an additional survival cost coupled to the white-mask phenotype, at equilibrium it should occur at lower levels than black masks. Under this framework, it is extremely interesting to revisit the correlations between plumage traits and the quality indices (Table 3.2). One of the few statistically significant results in that table was that white-faced males tended to have fewer insects in their crops than black-faced males. This is highly speculative because the observed difference between white- and black faced male insect-collecting abilities was indirect and was not tested in a replicate sample of birds. Nevertheless, the idea illustrates one type of dynamic that could maintain white-faced masks throughout all quelea populations at relatively static, but low, frequencies.

Conclusion

Plumage variation in male red-billed queleas offer a striking exception to the general rule that variation in sexually dimorphic breeding ornamentation functions in condition-dependent signaling of phenotypic quality. Since no plumage trait was able to predict quality, it appears that plumage color expression in this species is not particularly costly

Three alternate hypotheses possibly explain plumage polymorphism in queleas: neutral mutation, compatible-mate signaling, and individual identity signaling. Out of these three possibilities, identity signaling seems the most probable because aspects of quelea social biology make being recognizable a likely adaptation in this species. Queleas nest in dense, immense, fast-paced and highly synchronized colonies. Within the colonies, there are cohesive social groups of territorial males nesting in dense nest-neighborhoods, all interacting repeatedly with each other within a backdrop of a huge number of potential intruders

Acknowledgements

I thank my Dissertation Committee: S.T. Emlen, R. Hoy, H.K. Reeve, P.W. Sherman and D. Winkler, the Cornell Graduate School and the Exploration Society for financial support, the Board Members of the Malilangwe Trust for permission to work at the Malilangwe Private Wildlife

Reserve; the Whittalls for permission to work at the Save Conservancy (Humani); A.P Dale and D.J. Dale for a vehicle; G. Hill’s lab for the spectrometer readings; R. Hartley, P. Mundy and the staff at Malilangwe, for help in Zimbabwe; and S. Emlen, H. K. Reeve, P. Sherman and D. Winkler for comments on the manuscript. This work was conducted with approval from the Research Council of Zimbabwe, the Zimbabwe Dept. of National Parks and Wildlife Management, and the Cornell Center for Research Animal Resources.

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CHAPTER FOUR:

"Dear-enemy" recognition in red-billed queleas

Introduction

Neighbor-Stranger (or "dear-enemy") recognition (Wilson 1975; Temeles 1994) has been described in detail in territorial birds (reveiwed in Lambrechts and Dhondt 1995). Such recognition occurs when neighboring territorial males recognize each other and tolerate each other more than they do unfamilar birds. Almost all descriptions of "dear-enemy" have been based on recognition via vocal cues. In such systems territorial males are able to identify particular neighbors by the distinctive charactersitics of the neighbor's songs. If a focal male hears the song of a different male coming from a neighbor's territory, then the focal male will typically investigate and often attempt to chase away the intruder. The adaptive benefit of such recognition abilities is generally believed to be reduced time and energy wasted in needless aggression between neighbors. Since neighbors each have their own territory, potential competition between them is reduced. In contrast, males are more interested in intruder birds because such birds presumably pose a greater immediate threat towards a focal male's resources, such as his territory or his mate.

In chapters 2 & 3 I have described how the variable breeding plumage of red-billed queleas is not an indicator of quality; dispite being a bright, sexually dimorphic breeding ornament. As an alternative function, I have argued that plumage may be a signal of individual identity that is used in "dear-enemy" recognition between neighboring territorial males. The goal of this chapter is to provide observational information about breeding red-billed queleas that is relevant to this identity-signalling hypothesis. Specifically, I provide information on 1) the degree of breeding synchrony and nest density in colonies, 2) the distributions of the different plumage morphs within a colony; and 3) the nature of neighbor-stranger interactions between males at their nests during early phases of a colony cycle.

1) Colony synchrony and density

Methods

To obtain information on the degree of nesting synchrony between different nests, I monitored egg hatching in four separate breeding colonies occurring in Zimbabwe (Jan-Feb 1994; Feb-Mar 1995). I selected a random sample of nests at each colony (range of N's = 15 to 125 nests per colony) and then recorded the date that the eggs in those nests hatched. I defined a nest's hatch date as the day the first egg hatched (most nests' eggs hatch over a 2-3 day period). In one of the four colonies that I studied, I also identified the nest-males' plumage coloration (N=103 nests). I catagorized male plumage as either red-hued or yellow-hued, and as either white-mask or black mask (Chapter 2). For each colony I defined Day 1 as the day the first egg in the sample hatched.

To get a measure of overall breeding density in a quelea colony, I measured the distance to the nearest nest (wall-to-wall) in a sample of 60 nests from one breeding colony occurring at Malilangwe Trust, Zimbabwe (21˚03', 31˚53';Feb. 1997). This sample of nests had been chosen for routine nest monitoring in the colony and represents a random sample of nests.

Results

In all four colonies the degree of breeding synchrony was very high. All the eggs in an entire colony were found to hatch in 6 days or less (Figure 4.1). Since colony sizes were very large (all the colonies in this sample were 0.5 km long or more), the high degree of synchrony indicates that a breeding colony is comprised of thousands of birds that are at very similar breeding stages. Since hatching in quelea nests is asynchronous, taking place over a 2-3 day period, then the fact that all the eggs in the samples hgatched within 6 days indicates that different nests initiated laying within 1 to 3 days of each other.

There was no correlation between plumage color and date of 1st egg hatch (black vs. white: t=0.30, P=0.77; red vs. yellow: t=1.64; P=0.10). This suggests that males of particular color varieties were not more likely to obtain mates any earlier than other color varieties.

Nest density was very high. The average distance to the nearest nest was 15 cm (±11 cm, N=60, range = 3 - 60 cm).

2) Distributions of morphs within a colony

Methods

For a quantitative analysis of morph distributions, I randomly selected 54 groups of 5 adjacent nests each, all within a single breeding colony occurring at Malilagwe Trust (Mar 1996). The groups were scattered throughout a single breeding colony and located at variable heights in trees (2-10m) and variable positions within the colony (from central areas to the edges). For each nest in each group I catagorized the plumage of the nest-

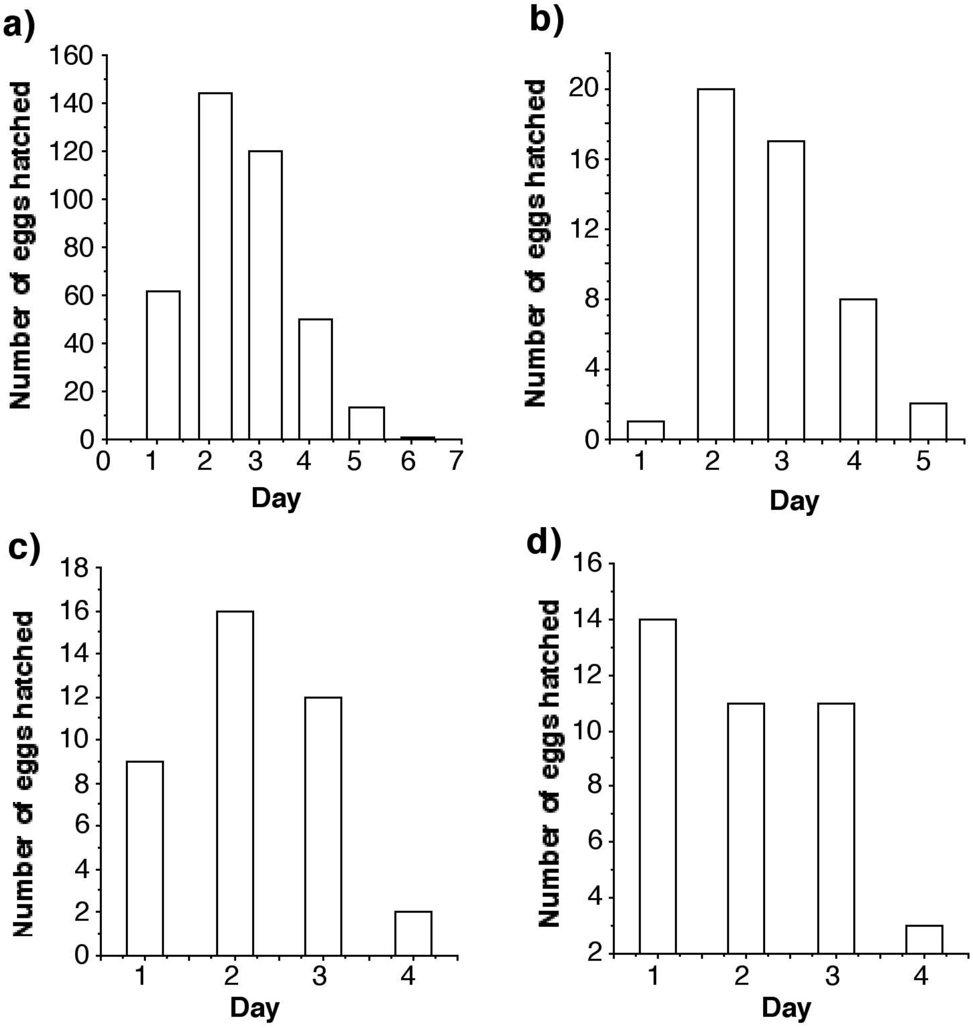

Figure 4.1. Hatching synchrony in 4 separate colonies of red-billed queleas breeding in Zimbabwe. In each colony, the vast majority of eggs hatch within a 3-4 day window.

male as either red or yellow and the shade of the mask as either white or black (Chapter 2).

I reasoned that if morphs associated with each other during nesting then the proportions of red-hued and white-masked males respectively would be significantly different from binomial distributions as calculated using the population-wide frequencies of the different morphs. For example if white-masked males tended to associate with each other, then groups of 5 nests would not demonstrate a binomial pattern; rather the distrbution would be comprised of groups of either all white-masked or all black-masked nest-males.

Results

The distributions of red-hued and white-masked males within the sample of nest-groups are plotted in Figure 4.2. These distributions were not different than the expected distributions calculated under the assumption that males were randomly assorting within the colony (Figure 4.2).

3) Neighbor Stranger Recognition

Methods

I collected data on neighbor-stranger recognition using videotapes of males at their nests at breeding colonies occurring at Malilangwe Trust, (Jan-Mar 1997). I recorded small groups of nests for two hour shifts using videocameras placed 5m or more from their nests. Since aggression at nests is highest during earlier colony stages; I only collected data from tapes of nests from late nest-building to early incubation (1-2 days after last egg).

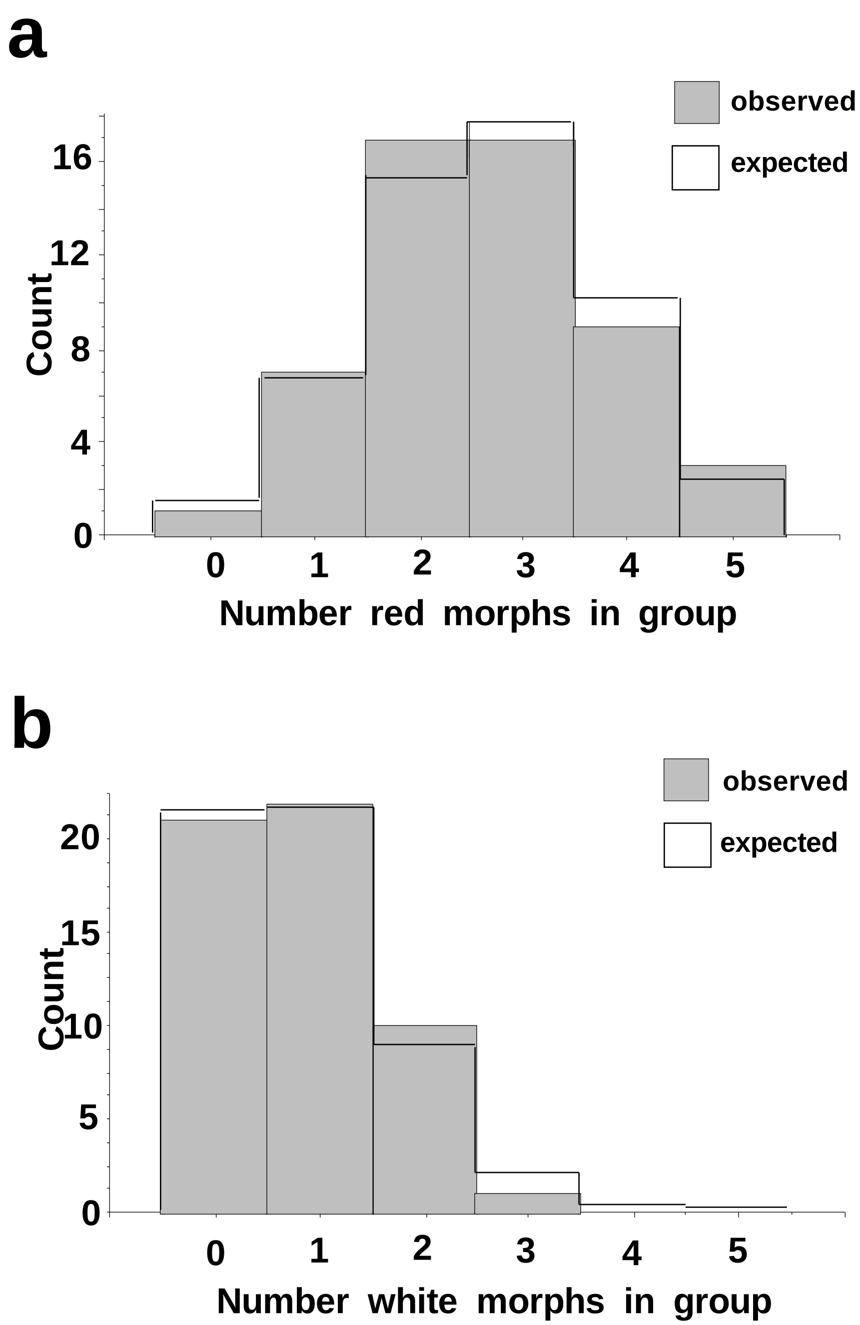

Figure 4.2. Proportion of **a)** red morphs and **b)** white morphs in 54 groups of 5 adjacent nests each. These proportions were not statistically different than the distributions expected if quelea color morphs assort themselves randomly within colonies: a) plumage hue, $X^2 = 0.52$, N=54 nest groups, df=5, P>0.90; b) mask shade, $X^2=0.66$, df=3, P>0.75. In the latter statistical test, I pooled the expected values for 3,4, and 5 white-mask males per group.

In total I recorded data from 5 focal males that I observed for 60 to 90 min each; and that were only observed during periods when the male was active and present within his nesting territory (i.e. not away foraging). I designated the territory of a male as the zone formed by all the available perches occuring around his nest that were occurring within a volume whose edges occurred at the locations of all the neighboring males's nests immediately adjacent to the focal nest and up to a maximum of 30 cm away. Thus, the focal male's territory was defined as a sphere of 45cm around the nest, with nearer borders allocated to any neigboring male's nest that occurred less than 45cm away. Throughout the observation period, I considered an intrusion to occur every time another male entered the focal male's designated territory. For each "intrusion" I recorded 1) the identity of the male as a neighbor or stranger, and 2) the response of the focal male. If there were multiple interactions with a male during a single intrusion, then the score for that intrusion was based on the highest degree of aggression that was realized by the focal male. A neighbor was any male in a nest occurring immediately adjacent to the focal male's nest, and was identified as such on the tapes using both distinctive plumage characteristics and diagnostic behaviorial cues (e.g. nest-building). Strangers were any other male, other than the neighboring males. Interactions with females and birds that just flew through a male's territory were not used in this analysis. The focal male's response was scored on a scale from 0 to 6 representing an increasing degree of aggression (Table 4.1).

Table 4.1. Levels of aggression recorded in responses by focal males towards territorial "intrusions".

Score	Level	Description
0	Ignore	No noticable reaction by the male
1	Bill-Thrust	Focal male rapidly jabs his bill towards the target
2	Threat	Male threatens target with a bill thrust and body lunge while his body is crouched in a forward position.
3	Advance	Male threatens and hops aggressively towards the target male, but not all the way up to the position of the target.
4	Displace	Male advances aggressively towards the target and occupies the position where the target was located.
5	Attack	Male advances towards the target and physically jabs him with his bill.
6	Chase	Focal male pursues the target male beyond the initial position of the target male.

Results

The overall rates of "intrusions" into the designated zone were high for all the focal males. On average, neighbors entered into the designated zone at a rate of 28.4 "intrusions" per hour. This is not particularly surprising as the edges of the observtion zone were often defined by the neighbors' nests. Thus neighbors would repeatedly enter into that area as they conducted routine behaviors at their own nests. The rate of intrusions by strangers was lower than it was for neighbors: 7.1 "intrusions" per hour. However, relative to territorial interactions occuring in other species of birds this rate of interaction represents a very high rate of persistent intrusions by a large number of different individual males.

Focal males actively responded to neighbor-male intrusions less often than they did to stranger-male intrusions. Focal males reacted aggressively 29.7% of time a neighbor-males entered into the designated zone around the focal males' nests. In contrast, focal males reacted aggressively to 91.2% of "intrusions" by stranger-males (Wilcoxon signed-rank test, N= 5 males, P=0.04).

Focal males responded much more aggressively towards strangers than they did towards neighbors. Typically, focal males would give mild threats towards neighboring males; usually in response to any sudden positional change by the neighbor-male. Elevated levels of aggression (e.g. attacks and chases) between neighbors and strangers did occur, especially when a neighbor got very close to a focal male's nest. However, these interactions represented a relatively small fraction of the total interactions that occured between the neighboring males. In contrast, focal males were much more aggressive towards stranger-males, often attacking and chasing them (Figure 4.3, paired t = 14.38, N=5, p<0.0001).

Discussion

The results presented here summarize aspects of quelea social biology that are relevant towards the identity signaling hypothesis. Quelea colonies are highly synchronized, dense and have a random distribution of male color varieties within them. Moreover, discrimination by nest-males of neighboring males vs. unfamilar males is strong. Nestmales are much more aggressive and are much more likely to react aggressively to unfamilar males than they are to neighboring males.

The high level of synchrony in colonies is important because it may increase the need for males to be as recognizable as possible. Males' nest-building behavior typicallly takes place for 3 days before egg-laying begins (Crook 1960). The nests within a colony are so synchronized that all the eggs in a colony hatch in a very short time window (4 to 7 days). Since hatching is asynchronous and occurs over a 2-3 day period for each nest, this indicates that the majority of the females of a colony initiate egg-laying over only a two day period. Therefore all the males are forming their territories and building their nests concurrently with each other in the 3 days prior to the egg-laying period. If "dear enemy" recognition is important to males, then it might pay a male to be as visually recognizable as possible under such a time-compressed and synchronous period of territory formation. Thus recognizability could result in decreased aggression received from neighboring males during this period. Indeed, males aggressively defend small areas around their nests, often chasing and threatening other males up to 0.50 m from their nests. The fact that nest density is so high (in this study the average nest had a neighbor only 0.15m away), then it would be particularly useful to be recognizable if it resulted in a large decrease in aggression from neighboring males. This is because a high nest density coupled with a large zone of protection around individual nests results in males who defend territories that actually overlap with the nests of their neighbors. Under such conditions, if a male were indiscriminable from intruders, then he would presumably experience very costly levels of aggression from neighboring males.

An important prediction of the identy-signalling hypothesis is that variability among neighboring nest-males must be high. If this were not the case, then being recognizable via plumage cues would be less likely because it would be easier to be confused with other nearby males. In other words, if males tended to nest in clumps of similar morph types, then recognition of different individuals would be more difficult. However, the results reported here demonstrate that males choose nest sites completely randomly with respect to neighboring male morphs.

It could be argued that the IR hypothesis predicts that males should actually space themselves out so that they maximize how different they are from their immediate neighbors. Such behavior would result in an even distribution of males and so the frequency distirubution of morph types within nest-groups would be narrower (less variable) than a simple binomial distribution. In order to accomplish this, males would need to be able to shop around for particular nest-territories that were bordered by males that were as dissimiler from themselves as possible. Such abilities in males would be costly because it would require time (which is in short supply in a quelea colony) and rather sophisticated cognitive skills. Nest space in a colony is

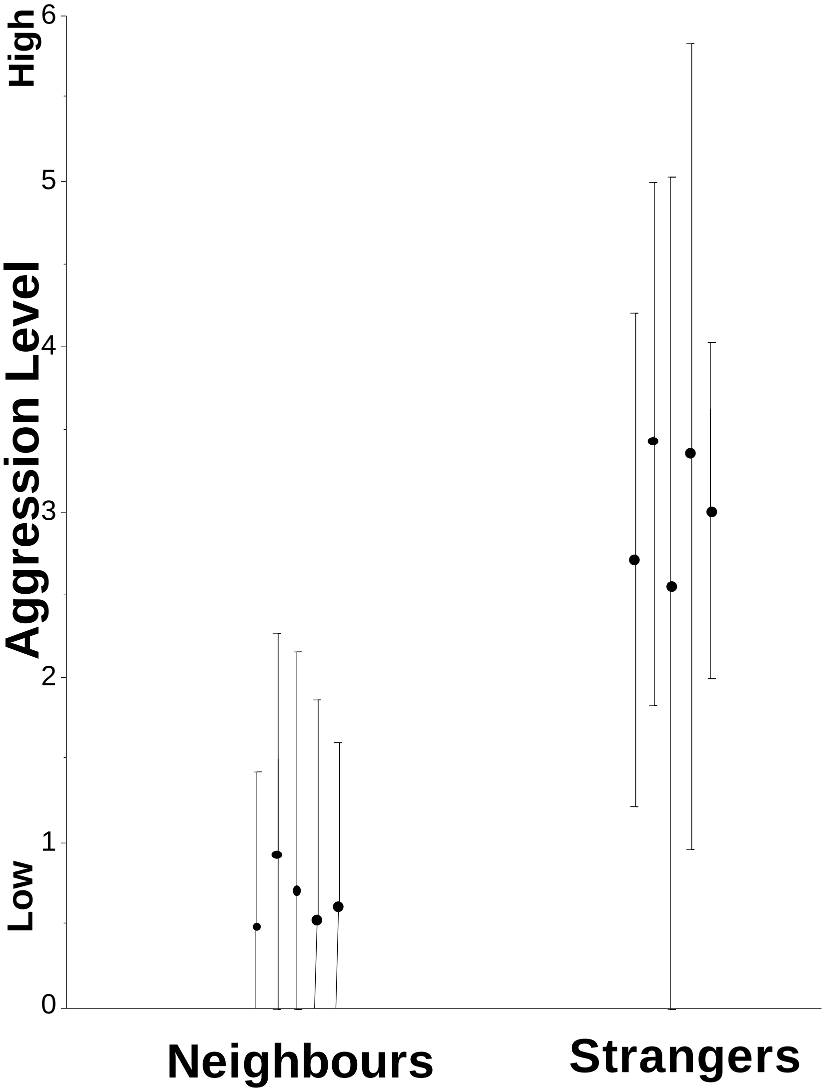

Figure 4.3. Mean ± s.d. level of aggression displayed by 5 focal males towards neighboring males and stranger males.

presumably quite limited and so males may not be able to afford to to search extensively for a territory bordered by dissimilar males. Such costs could drive the system to an equilibrium where overall variability between males is extremely high and males just settle randomly. As long as total variability is high enough such that neighboring males will be discriminable from each other, then this stratgey would suffice. Secondly, the important thing for a male may not to be discriminable from the other neighbors anyway; but from the immense number of potential stranger-males. Thus it might not necessarily matter what the other neighbors look like, but how you compare to the intruders. Nest males will tend to be more recognizable when overall population variability is extreme.

The results presented in this chapter 1) describe the socioecological conditions that may represent important factors favoring recognizability in red-billed quelea males, and 2) describe behavioral observations that suggest neighbor-stranger recognition occurs and is important in this species. Whether or not males are actually using plumage to discriminate neighbors from strangers is currently unknown; however plumage does provide obvious and reliable cues for such purposes. Further research on quelea recognition should focus on testing whether or not plumage is an important cue used for recognition (see chapter 7).

Acknowledgments.

I thank my Dissertation Committee: S.T. Emlen, R. Hoy, H.K. Reeve, P.W. Sherman and D. Winkler, the Cornell Graduate School and the Exploration Society for financial support, the Board Members of the

Malilangwe Trust for permission to work at the Malilangwe Private Wildlife Reserve; A.P Dale and D.J. Dale for a vehicle, P. Mundy and the staff at Malilangwe for help in Zimbabwe; and S. Emlen and D. Winkler for comments on the manuscript. This work was conducted with approval from the Research Council of Zimbabwe, the Zimbabwe Dept. of National Parks and Wildlife Management, and the Cornell Center for Research Animal Resources.

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VOL. 158, NO. 1 THE AMERICAN NATURALIST JULY 2001

Signaling Individual Identity versus Quality: A Model and Case Studies with Ruffs, Queleas, and House Finches

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Submitted January 21, 2000; Accepted February 23, 2001

ABSTRACT: We develop an evolutionary model that predicts that characters selected to signal individual identity will have properties differing from those expected for indicator signals of quality. Traits signaling identity should be highly variable, often display polymodal distributions, not be condition dependent (i.e., be cheap to produce and/or maintain), not be associated with fitness differences, exhibit independent assortment of component characters, and often occur as fixed phenotypes with a high degree of genetic determination. We illustrate the existence of traits with precisely these attributes in the ornamental, conspicuously variable, and sexually dimorphic breeding plumages of ruff sandpipers *Philomachus pugnax* and red-billed queleas *Quelea quelea*. Although ruffs lek and queleas are monogamous, both species breed in high-density aggregations with high rates of social interactions (e.g., aggression and territory defense). Under these socioecological conditions, individual recognition based on visual cues may be unusually important. In contrast to these species, we also review plumage characteristics in house finches *Carpodacus mexicanus*, a nonterritorial, dispersed-breeding species in which plumage ornamentation is thought to signal quality. In keeping with expectations for quality signals, house finch plumage is relatively less variable, unimodally distributed, condition dependent, correlated with fitness measures, has positively correlated component characters, and is a plastic, environmentally determined trait. We briefly discuss signals of identity in other animals.

Keywords: individual recognition, identity signals, quality indicators, signal properties, plumage color, sexual selection.

Individual recognition (IR) occurs when an organism identifies another individual according to its distinctive characteristics. Precision of IR depends on the individual distinctiveness of the recognition cues, with the maximum level of precision occurring when every individual has unique cues. Since IR can play crucial roles in a wide variety of social contexts (e.g., mate recognition, kin recognition, dominance hierarchies, delayed reciprocal altruism, and neighbor-stranger discrimination), one might expect the ability to recognize individuals to be a widespread characteristic of social species (e.g., Barnard and Burk 1979; van Rhijn and Vodegel 1980; Beecher 1982; Ydenberg et al. 1988; Johnstone 1997). Indeed, both observational and experimental evidence has shown that birds (e.g., Whitfield 1987; Lambrechts and Dhondt 1995), fish (e.g., Höjesjö et al. 1998), mammals (e.g., Halpin 1980; Sayigh et al. 1999), reptiles (e.g., Olsson 1994), and invertebrates (e.g., Karavanich and Atema 1998) regularly identify particular individuals. Further, these studies have demonstrated that IR cues can occur in several different sensory modalities, especially sound, smell, and sight (Wilson 1975; Sherman et al. 1997; and references cited above).

Individual recognition involves a sender-receiver dyad; therefore, how selection affects the ability to be recognized easily (sender) must be distinguished from how selection affects the ability to accurately recognize others (receiver; Beecher 1982, 1989; Johnstone 1997; Sherman et al. 1997). For example, territory owners (receivers) may be under strong selection to be able to learn, remember, and identify neighboring residents (senders) independent of whether selection favors the senders to actively broadcast their identity. However, if the senders do benefit by being identifiable, for example, through decreased aggression received from neighboring individuals, then selection should favor senders who communicate their identity by producing individually distinctive cues. Thus, when IR is invoked to explain high population variance in signal characters (e.g., Collias 1943; Tschantz 1959; Watt 1986; Whitfield 1986; Medvin et al. 1993), this implies that the signalers must benefit by being identifiable. Conversely, a lack of dramatic variation does not imply that IR is not

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Am. Nat. 2001. Vol. 158, pp. 75–86.

occurring because selection can improve a receiver's ability to discriminate finer degrees of phenotypic variation. Although studies on receivers' abilities to discriminate individuals are common, few researchers have considered specifically the problem faced by senders who wish to broadcast their individual identity (but see Beecher 1982, 1989 for notable exceptions).

Signaling Quality

Individuals may also be selected to broadcast information about their quality (Andersson 1994). For example, many of the signals that individuals might employ to attract mates (i.e., courtship displays, bright coloration, ornamentation, pheromones) are thought to reveal the overall constitution of the signaler (e.g., its physical condition, parental care abilities, territory quality, age, experience, good genes, and freedom from disease). Receivers of these signals are selected to pay attention to those characters that reliably predict quality because receivers gain fitness benefits by choosing good mates. Theories of sexual selection have converged on the idea that signals of quality should be costly to produce and/or maintain. Such signals are "honest," that is, reliable indicators of quality, because low-quality individuals are unable to afford the costs associated with extensive trait elaboration (e.g., see Zahavi 1975; Kodric-Brown and Brown 1984; Kirkpatrick and Ryan 1991; Andersson 1994; Olson and Owens 1998).

Signals that indicate quality are expected to express high degrees of phenotypic variation, at least when compared to the levels of variation normally observed in non–sexually selected morphological characters (Kodric-Brown and Brown 1984; Alatalo et al. 1988). This is because individuals should vary in their ability to afford the costs of signal elaboration; without variation in relative costs, receivers would not be favored to pay attention to the signals. Consequently, the signal elaboration itself should vary, reflecting those variable costs (Alatalo et al. 1988; Andersson 1994). Since high variation can occur in quality indicators, and is also predicted for signals of individual identity, variation alone is insufficient to discriminate between these two types of signals.

Objectives

Here we develop a simple mathematical model to predict the properties of signals that have been selected to advertise the individual identity of the senders (identity signals). Our model makes the simple assumption that there is a net benefit for senders to provide identity cues (e.g., see Johnstone 1997) and uses a game theory approach to assess signal properties at the selective equilibrium. Based on the findings of our model, verbal extensions of it, and ideas from the literature, we summarize and compare the expected properties of identity signals to the expected properties of signals that have been selected to reveal information about quality (quality signals).

In light of these arguments, we then review characteristics of the sexually dimorphic breeding plumages of ruff sandpipers *Philomachus pugnax* and red-billed queleas *Quelea quelea*, two bird species whose extremely variable plumages have been argued as likely candidates for identity signals (ruffs: Hogan-Warburg 1966; van Rhijn 1991; queleas: Dale 2000*a*, 2000*b*). We also summarize the patterns of plumage coloration in house finches *Carpodacus mexicanus*, a species for which there is convincing evidence that variation in plumage coloration functions in quality signaling (G. E. Hill 1991, 1992; Hill and Montgomerie 1994; Thompson et al. 1996). In contrast to the plumage properties in house finches, the properties of both ruff and quelea plumage are more consistent with identity signaling than quality signaling. Thus, ruffs and queleas provide striking exceptions to the commonly held view that variation in ornamental breeding coloration functions as a signal of quality. Although we concentrate on variation in plumage color, the patterns reported here are expected to be general and should offer insight into identity signaling in all sensory modalities in all taxa.

Model

Suppose that there are two distinct color morphs, say red and yellow, and that the relative frequency of the red morph is q. For simplicity, an individual's morph is assumed to be independent of its quality. Suppose that each individual interacts with a total of n other individuals. Further suppose that a focal individual experiences an expected cumulative fitness cost c (relative to a standard fitness unit of 1.0) as the result of a given group member confusing the focal individual with another individual in the group and that such confusion occurs only when the focal individual has the same color as another group member. For example, such a cost may arise when a low-ranked group member has been mistaken for a more highly ranked group member (i.e., a greater reproductive threat) and has received especially intense aggression from a dominant group member. Alternatively, the cost may arise when the focal individual is a territorial neighbor that has been mistaken as an intruder.

Note that some mistakes could benefit a focal individual, for example, if an intruder is mistakenly treated as a territorial neighbor, enhancing the intruder's ability to steal nest material or usurp the nest from the misperceiving resident. We require only that, at the moment when identity signals are generated, there is a net future cost to being mistakenly treated when the fitness effect of being mistakenly treated is averaged over all interactants. This assumption may be most accurate when the number of territorial residents in the group of interactants is larger than the number of intruders in the group of interactants. More rigorously, let there be a fraction f of individuals who reap an overall mean benefit b from being confused with another individual, but the remaining fraction experiencing a mean fitness cost c. In such a case, there will be an overall mean fitness difference equal to $fb - (1 - f)c$ for individuals that signal their individual identities, and thus IR signaling will spread if $f < c/(c + b)$. Thus, if the fraction of individuals benefiting from confusion over identity (or if the magnitude of this benefit) is sufficiently small, then identity signals will begin to spread.

For simplicity, we initially assume that the expected total cumulative fitness cost of being mistakenly treated is linearly positively related to the number of group members having the same color as the focal individual. Let m be equal to the number of other group members having the same color as the focal individual. We thus can represent the overall fitness of a red morph as $1 - cm$, where c is a constant and the fitness of a morph not experiencing any mistaken treatment by other group members is standardized as unity. Thus, if groups form randomly, the expected fitness of a red individual is equal to

$$1 - c\bar{m} = 1 - cnq. \tag{1}$$

By symmetry, the fitness of the yellow morph is $1 - cn(1 - q)$. The red morph always invades a population of yellow morphs (and vice versa). When yellow morphs predominate, q is near 0, so the fitness of a red morph is approximately 1, whereas that of the yellow morph is only $1 - cn$. This reciprocal invasion occurs because a rare morph will always be discriminable from the other morphs in the group and thus, unlike the predominant morph, does not have to pay any costs for being confused with other group members. At the evolutionarily stable state, the fitness of the red morph will equal the fitness of the yellow morph (Maynard Smith 1982). From the latter, it follows that the equilibrium frequency of red morphs q^* will be one-half.

This conclusion can easily be generalized for arbitrary (nonlinear-cost) fitness functions and any number of alternative morphs. Let the fitness of the *ith* morph be described by a function $w(p_i)$ of the relative frequency p_i of the *ith* morph. Since w has the same mathematical form for each trait, there must be an equilibrium at $p_1 = p_2 = \ldots = p_s = 1/s$ for each of the s morphs because, at these frequencies, the fitnesses of the morphs will be equal ($= w[1/s]$). The stability of the equilibrium is guaranteed if the fitness of each morph declines as its frequency increases, that is, $\partial w(p_i)/\partial p_i < 0$, as assumed in the IR model. To see this, let the frequency of an arbitrary morph be perturbed by a small amount x from the equilibrium frequency $1/s$. By a first-order Taylor expansion, the fitness of the morph is equal to $w(p_i + x) \approx w(p_i) + x\partial w(p_i)/\partial p_i$. Since $\partial w(p_i)/\partial p_i < 0$, the fitness of the morph will be lowered if its frequency is perturbed upward ($x > 0$) and be increased if its frequency is perturbed downward ($x < 0$), with the result that selection always acts to restore the equilibrium frequency.

It may be that one color is more costly than the other to produce. Alternatively, the morph of one color may be more vulnerable to predation than the alternative color morph. Suppose the red morph in the IR model with linear costs pays an additional cost a compared to the yellow morph, such that the fitness of the red morph becomes $1 - a - cnq$. The red morph will be able to spread in a population of yellow morphs if $1 - a > 1 - cn$ or $a < cn$. If the red morph spreads, the equilibrium frequency of the red morph is equal to

$$q^* = \frac{cn - a}{2cn}. \tag{2}$$

The equilibrium frequency q^* of the red morph declines as its extra cost a increases and increases as the number of interactants n increases (fig. 1). If c is sufficiently large, satisfying $a \ll cn$, the equilibrium frequency of the red morph asymptotically approaches one-half as the number of interactants n becomes large (fig. 1); however, the equilibrium frequency of the red morph can be substantially below one-half if c is small (fig. 1).

In general, the above results illustrate that selection to signal individual identity will increase phenotypic variation because selection for rare phenotypes (negatively frequency dependent selection) should result in an increase

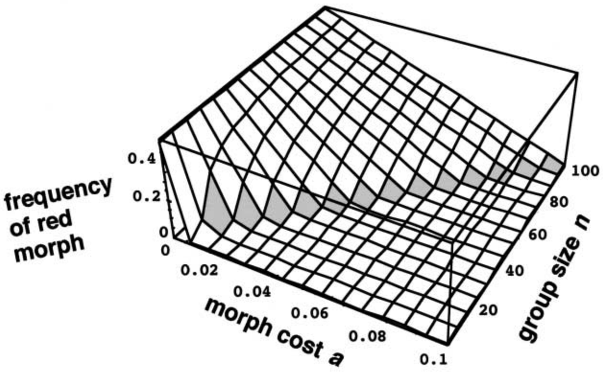

Figure 1: Equilibrium frequency of the red morph as a function of the morph cost (a) and the number of group members n; $c = 0.001$.

in overall variability at equilibrium. Furthermore, variance in identity signals will increase as the number of interacting individuals increases (Beecher 1989; fig. 1). Selection for identity signals is similar in many ways to diversifying selection causing polymorphism in histocompatibility loci (for which there is an obvious advantage to signaling individual identity to oneself), except that the phenotypic diversification is among rather than within individuals. In contrast, strong directional selection operating on quality signals should not enhance phenotypic variation. Quality signals are still expected to have higher phenotypic variance than are non–sexually selected morphological characters (Kodric-Brown and Brown 1984; Alatalo et al. 1988). However, we argue that due to the negatively frequency dependent selection favoring rare phenotypes under identity signaling, identity signals have a greater potential for high variability than quality signals.

Furthermore, under identity selection, uniform, complex, or multimodal distributions can occur because negatively frequency dependent selection can readily result in polymorphisms (Maynard Smith 1982). At equilibrium, the realized distribution of an identity signal will depend on the pool of available alleles and the relative costs associated with expressing them (in the absence of information about these costs and constraints, it is not possible to generate an expected frequency distribution). In contrast, quality signals usually have unimodal frequency distributions (e.g., Alatalo et al. 1988; Hill 1992; Wolfenbarger 1999). Such unimodal distributions presumably arise from unimodal distributions of the overall quality underlying the expression of those signals (since it is likely that a great many loci will affect an individual's overall quality, quality is likely a quantitative trait, and it should therefore generally display unimodal distributions).

Identity signals should not be particularly costly, otherwise they will not rise to high enough frequency to contribute appreciably to individual variation (see eq. [2]). This prediction contrasts strongly with that for costs associated with expressing quality. The honesty of quality indicators is necessarily linked with their high production or maintenance costs, and therefore we expect that quality indicators will tend to have high costs (Kodric-Brown and Brown 1984). In sum, we expect the expression of identity signals to be largely independent of phenotypic condition (since their costs will be generally low), whereas expression of quality signals will be dependent on the phenotypic condition of their bearers (since their costs will tend to be high).

The individual identity model also predicts that different signal variants will have equal fitnesses, as this is required for different variants to persist at the selective equilibrium. In contrast, quality signal variants are expected to have unequal fitness. The fitness associated with the signal variant of a high-quality individual should exceed the fitness associated with the signal variant exhibited by a low-quality individual because the former pays smaller net costs and/or reaps greater net benefits by signaling.

Given that an individual identity polymorphism has arisen as described by our model, how will subsequent evolution affect the phenotypic correlation among multiple polymorphic characters? Beecher (1982) argued that the most efficient way to broadcast individual identity is to have signals based on multiple variable characters that are uncorrelated to each other. Indeed, under the IR model developed above, selection will favor maintenance of a zero correlation between two characters.

To see this, let the frequencies of the four distinct morphs generated by a dual dimorphism (i.e., two traits with two equally frequent morphs each) be equal to $f_1 = (1/4) + x$, $f_2 = (1/4) - x$, $f_3 = (1/4) + x$, and $f_4 = (1/4) - x$, with x measuring the departure from random association of the two traits (i.e., the degree of linkage disequilibrium). Let x be the target of selection, that is, genotypes exist that can modulate the value of x. We take into account the distribution of the traits in offspring, averaging over all parents who had a given value of x. Following Maynard Smith (1982), we first describe the mean fitness of a rare mutant genotype playing $x = x'$ in a population in which a majority (a fraction $1 - u$) exhibits $x = 0$ and in which a small minority (a fraction $u \ll 1$) plays $x = x'$. From the IR model developed above, this fitness is equal to

$$\begin{aligned} W(x', 0) &= \sum_{i=1}^{4} f_i\{1 - cn[uf_i + (1 - u)(1/4)]\} \\ &= 1 - (1/4)cn[1 + 16m(x'^2)], \end{aligned} \tag{3}$$

where the x in f_1–f_4 is set equal to x'.

The evolutionarily stable value of x is 0, provided

$$\left.\frac{\partial W(x', 0)}{\partial x'}\right|_{x'=0} = 0 \tag{4}$$

and

$$\left.\frac{\partial^2 W(x', 0)}{\partial x'^2}\right|_{x'=0} < 0. \tag{5}$$

Indeed, $\partial W(x', 0)/\partial x' = -8cmnx'$, satisfying (4) and $\partial^2 W(x', 0)/\partial x'^2 = -8cmn$, satisfying (5), because c, m, and n are all positive. Thus, the stable value of x is 0, and selection maintains a zero correlation between the two traits. This prediction contrasts with the corresponding prediction of quality signaling models, in other words, that

Table 1: Summary of the general properties (at equilibrium) of traits that signal individual identity versus traits that signal quality

Trait properties	Identity signals	Quality signals
Variability	Relatively high	Relatively low
Frequency distributions	Complex	Unimodal
Condition dependence	Not related	Condition dependent
Correlations with fitness	Trait values not related	Trait values correlated
Intercorrelations	Independence of characters	Characters correlated with each other
Genetic determination	Relatively higher degree of genetic determination	Relatively higher degree of environmental determination

quality indicators should tend to positively co-vary under the assumption that they signal, at least in part, common aspects of an individual's overall phenotypic constitution (Kodric-Brown and Brown 1984; Møller and Pomiankowski 1993).

A corollary of the prediction of zero intercorrelation among identity signals is that such traits should be especially likely to have a high degree of genetic determination (i.e., heritability in the broad sense; Falconer and Mackay 1996). That is, one easy (i.e., noncostly) way to establish a zero correlation among traits is to have them under the control of genes on different chromosomes or in complete linkage equilibrium if they are under the control of loci on the same chromosome. In such a case, Mendelian independent assortment automatically generates the zero correlation that is theoretically favored. It is important to stress that other mechanisms also could give rise to variable cues that function as identity signals (Beecher 1982; Randall 1995). A possible, but seemingly less likely, route for generating zero intercorrelations among an identity signal is to have its component traits randomly expressed in different environments. However, unless the environmental triggers are completely random, the signal diversity will be less optimal than that produced by selection on biallelic signal variants located on two unlinked loci. Another possible mechanism that could give rise to variable and uncorrelated traits is for signalers to learn to produce distinctive behavioral cues (Beecher 1982; Randall 1995). However, this mechanism might be comparatively more costly, and hence rarer, than simple genetic determination because its expression requires additional cognitive adaptations, and flexible behavioral signals are vulnerable to copying by intruders.

In contrast, components of quality signals are not favored to have zero intercorrelation since they all are tied to quality. First, there is no intrinsic advantage to having the components under the control of different chromosomes. Second, condition dependence of quality signals will reduce the degree of genetic determination of such traits because any nongenetic factor that influences condition, such as environmental factors, will also affect the expression of condition-dependent signals. In sum, the model predicts that identity signals should tend to exhibit (although not invariably) higher degrees of genetic determination than should quality signals.

Model Summary and Predictions

We expect that identity signals will generally have properties that are distinct from quality signals (table 1). We do not argue that identity and quality signaling are necessarily mutually exclusive. If quality signals are variable enough, they could also play a role in IR (note that identity selection would then possibly provide some benefit to those who express ornaments that signal low quality). We do argue that the effects of these two selection processes are different. As such, we expect that under socioecological conditions where there is a particularly strong benefit to being individually recognized (or, equivalently, a large cost to not being recognized), one will be particularly likely to encounter signal characters with the properties of identity signals outlined above.

Case Study Species

In light of the above ideas, we review the properties of the colorful plumage ornamentation in three distantly related species: ruff sandpipers, red-billed queleas, and house finches. Plumage colors in ruffs and queleas are argued to be candidate identity signals (Hogan-Warburg 1966; van Rhijn 1991; Dale 2000*a*, 2000*b*; Lank and Dale, in press), while plumage color in house finches is generally argued to be a condition-dependent signal of phenotypic quality (G. E. Hill 1991, 1992; Hill and Montgomerie 1994; Thompson et al. 1996).

Ruffs

Ruffs are lekking sandpipers (Scolopacidae) that breed in the Palearctic following a northward migration (Hayman et al. 1986). Within days of arrival on the breeding grounds, most adult males aggregate at leks, where they establish approximately 0.3-m-diameter mating courts, located only 1–2 m apart, that they defend against most other breeding males. About 15% of males pursue a genetically determined alternative "satellite" strategy (Hogan-Warburg 1966). They move extensively among leks, and share courts with "independents," the territorial males who form the leks (Hogan-Warburg 1966; Lank et al. 1995). Prior to breeding, both kinds of males molt from a drab brown plumage into a colorful and ornamental plumage comprising a conspicuous and long ruff that extends from the neck, and head tufts that extend back from the crown. Color variation in these traits is based on melanin pigmentation and satellites tend to have lighter-colored plumages than independents (Hogan-Warburg 1966).

Red-Billed Queleas

The red-billed quelea (Ploceidae) is an abundant avian agricultural pest of sub-Saharan Africa (Bruggers and Elliott 1989). During the rainy season, huge numbers of these weavers nest in highly synchronized breeding colonies that are initiated when males begin weaving blades of grass into hanging globular nests (Crook 1960; Ward 1964). Queleas nest monogamously, and both sexes share about equally in parental care duties (incubation and feeding); however, it is the male alone that builds the nest and defends a small territory around it. Quelea colonies are dense, with pairs of nests often touching each other. During the nonbreeding season, queleas are sexually monomorphic and drab brown. However, for breeding, male queleas molt into a colorful plumage comprised of a melanin-based face mask that ranges in shade from black to white, and a carotenoid-based plumage framing this face mask that ranges in hue from red to yellow (Ward 1966; Dale 2000*b*).

House Finches

House finches are socially monogamous North American passerines (Fringillidae). This species nests in vegetated areas under mostly dispersed conditions (>5 m apart; Hill 1993). Females perform most of the nest building and all the incubation, but the male regularly brings food to the incubating female. Both sexes participate about equally in feeding the nestlings. House finches feed their chicks seeds that are obtained away from their breeding site. This may explain why house finches are nonterritorial and do not defend resources around their nests. House finches only have one molt per year, and males are more brightly colored than the drab-brown females. Male plumage coloration is based on carotenoid pigments that are deposited in feathers on the crown, ventral region, and rump. This plumage varies in hue, ranging from dull yellow to deep red, and patch size, the extent of pigmented feathers on the ventral region (Hill 1993).

Properties of Plumage Color in Ruffs, Queleas, and House Finches

In this section we review the plumage characteristics of the three study species with regard to the six model predictions discussed above and listed in table 1.

Variability

The elaborate breeding plumages of ruff males are the most variable feather tracts, in color and pattern, of any species of nondomesticated bird. Their ruffs and head tufts range from white through rust to black (fig. 2*A*). Further variation, not reviewed in detail here, arises from ruff and head tuft patterns (which can be solid colored, flecked, barred, or patchy in both regular and irregular arrangements; Hayman et al. 1986), the shade of secondary and tertiary ruff and head tuft colors, back and flank coloration, facial wattle color, bill color, and leg color (van Rhijn 1991; Lank and Dale, in press).

The breeding plumage of red-billed queleas probably represents the second most variably colored plumage in a wild species. Body plumage hue varies from deep red to pale yellow, and mask shade varies from jet black to pure white (fig. 2*B*). Further variation, not reviewed in detail here, stems from highly variable patch size and mask shape (Dale 2000*a*, 2000*b*). Thus, any individual male in either ruffs or queleas has the potential of being easily recognized by the uniqueness of its plumage.

House finches too, are quite variable in appearance. Plumage color ranges from drab yellow to bright red, and the size of the carotenoid patch on the ventral region is also quite variable (fig. 2*C*). House finches may represent an extreme with respect to variation in condition-dependent coloration. For example, plumage color in male cardinals *Cardinalis cardinalis* (Wolfenbarger 1999) also appears to be an honest indicator of quality, yet intrasexual phenotypic variation in this character is comparatively less striking. Nevertheless, even house finch variability is relatively low when compared with the extreme variability present in ruffs and queleas.

Frequency Distributions

In both ruffs and queleas, plumage traits have unusual frequency distributions (fig. 2*A*, 2*B*; Dale 2000*b*; Lank and Dale, in press). In ruffs, both ruff shade and head tuft shade have complex multimodal distributions, with high frequencies of predominantly black feather tracts and a

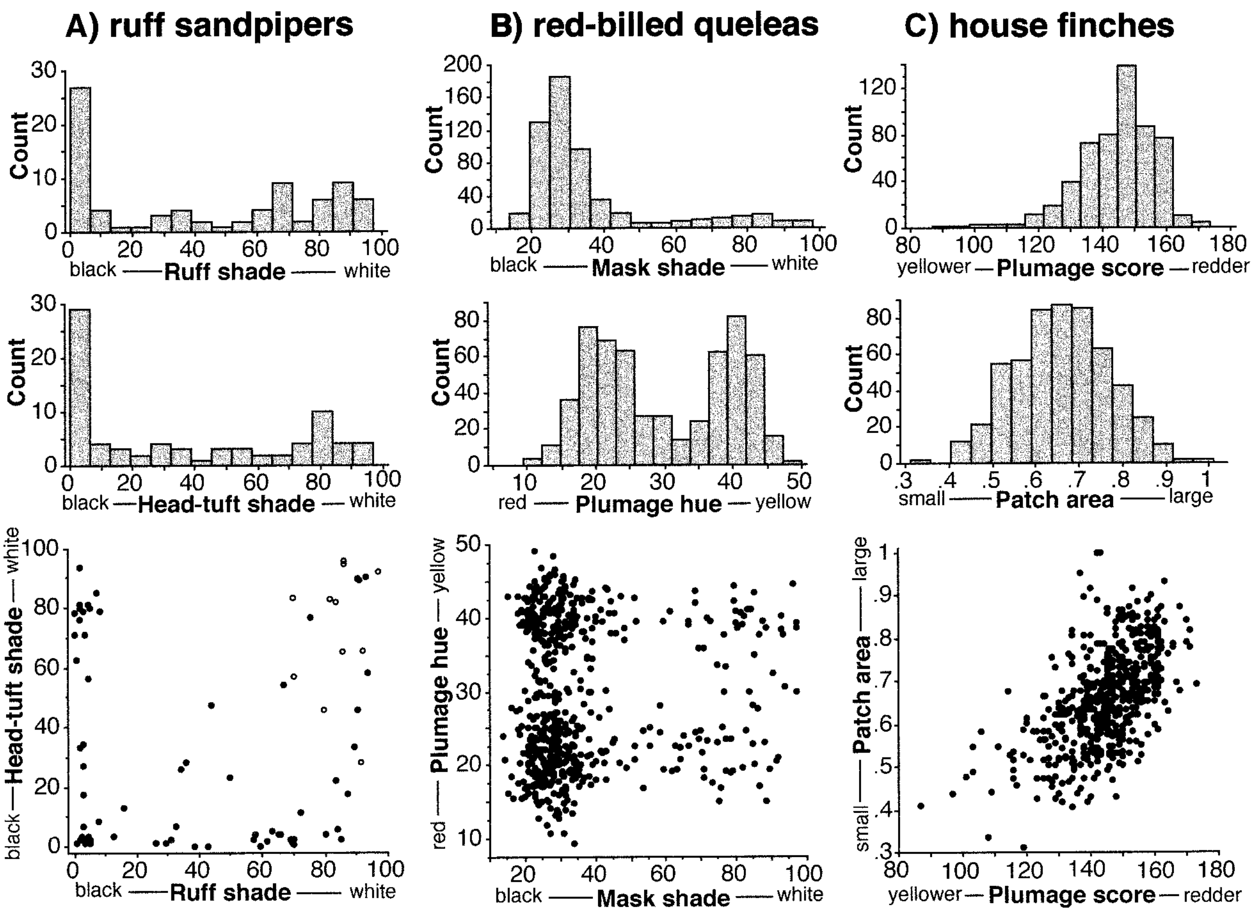

Figure 2: Comparison of plumage characters in the three study species. *A*, Ruff sandpipers; data on 77 wild males (65 independents, *filled circles*, and 12 satellites, *open circles*) caught near Oulu, Finland, from Lank and Dale (in press). *Upper panel*, frequency distribution of ruff shade; *middle panel*, frequency distribution of head tuft shade; *lower panel*, intercorrelation between ruff shade and head tuft shade ($rs = 0.14$, $P = .21$). Similar results are obtained if independents are analyzed separately (Lank and Dale, in press). *B*, Red-billed queleas; data on 573 wild males caught near Chiredzi, Zimbabwe, from Dale (2000*a*). *Upper panel*, frequency distribution of mask shade; *middle panel*, frequency distribution of plumage hue; *lower panel*, intercorrelation between mask shade and plumage hue ($rs = 0.003$, $P = .93$). *C*, House finches; data on 548 wild males caught at Ann Arbor, Michigan, from Hill (1992). *Upper panel*, frequency distribution of plumage score; *middle panel*, frequency distribution of patch area (i.e., percentage of ventral region pigmented); *lower panel*, intercorrelation between plumage score and patch area ($rs = 0.57$, $P = .0001$). Details on the quantification of the different color values are provided in the original articles.

wide spread across other shades (fig. 2*A*). In queleas, plumage hue and mask color are continuous but have pronounced bimodal patterns (fig. 2*B*). In strong contrast, the two plumage characters in house finches are unimodally distributed (fig. 2*C*; Hill 1992).

Condition Dependence

An analysis of plumage color and size in ruffs shows that lighter colored males are, on average, smaller than darker colored birds (Höglund and Lundberg 1989). However, this occurs because the satellite morphs are both lighter colored and slightly smaller than independents. The size difference reflects an adaptation to the different requirements of independents and satellites during the mating season rather than poorer growth when young or below average body condition (Lank and Smith 1987; Lank et al. 1995; Bachman and Widemo 1999). For example, independents need to be larger and have a larger nutrient storage capacity than satellites because they defend territories and have fewer foraging opportunities during breeding (Lank and Smith 1987; Lank et al. 1995; Bachman and Widemo 1999). Furthermore, plumage color is fixed for life and expresses the full range of plumage values in males reared in captivity. Such characteristics argue against the idea that ruff plumage coloration is associated with variation in phenotypic condition.

In queleas, plumage expression is independent of phenotypic condition. Dale (2000*a*, 2000*b*) analyzed large samples of males (>800 individuals) and found no significant relationships between plumage coloration and a variety of measures of phenotypic condition. These measures (all of which varied unimodally; Dale 2000*a*) included mass standardized by tarsus length, wing length, bill length, tarsus length, combined testis volume, and length of feather growth bars. This suggests that the costs of producing different plumage varieties are relatively small, since males are able to express all varieties regardless of their condition.

In contrast to ruffs and queleas, plumage color in house finches is strongly condition dependent. Redder house finches tend to molt earlier and faster (Hill and Montgomerie 1994), are on average older (Hill 1992), have greater overwinter survival (G. E. Hill 1991), have greater feeding rates at their nests (G. E. Hill 1991), have fewer parasites (Thompson et al. 1996), and are larger in terms of mass controlled for by skeletal size, wing length, and bill length (G. E. Hill, personal communication).

Correlations with Fitness

In ruffs, male mating success is expected to be a major component of male fitness in this classically lekking species. However, all six studies addressing this issue agree that plumage coloration is uncorrelated with mating success (Selous 1906–1907; Hogan-Warburg 1966; Shepard 1975; W. Hill 1991; van Rhijn 1991; D. B. Lank and C. M. Smith, unpublished data). Unfortunately, no data have yet been presented on male survivorship with respect to color.

Similarly, in queleas, preliminary evidence suggests there is no relationship between plumage color and fitness. Plumage color did not predict mean nestling number per male in large samples of nests (>700; Dale 2000*b*).

House finches contrast with ruffs and queleas because plumage color is strongly correlated with fitness. Redder males are more preferred as mates by females (G. E. Hill 1991), breed earlier (G. E. Hill 1991), have better overwinter survival (G. E. Hill 1991), have higher survivability during disease outbreaks (Nolan et al. 1998), and have higher seasonal reproductive success than do yellower males (McGraw et al. 2001).

Intercorrelations

As expected for identity signals, but not for signals of quality, plumage characters do not correlate with each other in ruffs and queleas (fig. 2*A*, 2*B*, *lower panels*; Dale 2000*b*; Lank and Dale, in press). In ruffs, both ruff and head tuft shade have similar distributions with biases toward black coloration, but black in one component is not correlated with black in the other, indicating that these two characters assort independently (fig. 2*A*, *lower panel*). Similarly, in queleas, plumage hue assorts independently of mask shade (fig. 2*B*, *lower panel*). Thus, for both species, the combination of the independent characters reviewed here, and the presence of many other polymorphisms that generally also assort independently, results in an incredible array of possible plumage patterns (ruffs: van Rhijn 1991; Lank and Dale, in press; queleas: Dale 2000*a*, 2000*b*). In strong contrast, plumage brightness in house finches is strongly and positively correlated with patch size (fig. 2*C*, *lower panel*; Hill 1992).

Genetic Determination

Plumage color in ruffs appears to be a developmentally fixed, genetically determined character whose expression is independent of environmental parameters. First, captive ruffs display the full range of color varieties that are expressed in the wild (D. B. Lank and C. M. Smith, unpublished data). Second, in both banded wild birds and captive birds, the color of each male's plumage remains the same from year to year (van Rhijn 1991; D. B. Lank and C. M. Smith, unpublished data). And third, examination of pedigree data, including the induction of male plumages in females through testosterone implantation, shows that plumage coloration and patterns are substantially and particulately heritable (Lank et al. 1995, 1999; D. B. Lank and C. M. Smith, unpublished data).

Similar patterns are apparent in queleas. First, captive queleas fed on a basic diet exhibit the full spectrum of morph varieties observed in wild populations. Second, captive males molt into similar breeding plumages over successive years, demonstrating that male plumage is a fixed, developmentally stable trait that is immune to influences such as age or diet. And third, the breeding plumages of captive raised offspring are similar to the plumage of their wild fathers, suggesting that plumage has a high degree of genetic determination based on inherited alleles at polymorphic loci that code directly for plumage color (as opposed to the pleiotropic effects of inherited viability genes; Dale 2000*b*).

Signals of quality are also expected to have some degree of father-son similarity (Kodric-Brown and Brown 1984; Andersson 1994). Indeed, in wild house finches, the plumage color of male offspring is significantly and positively correlated to the plumage color of their father (G. E. Hill 1991). However, plumage color in house finches contrasts with ruffs and queleas because it is plastic and significantly environmentally determined. First, house finches tend to develop increasingly redder plumage as they age (Hill 1992). Second, males maintained in captivity on a seed-only diet all converge onto a similar drab yellow coloration (Hill 1992). Moreover, when their diet is supplemented with additional carotenoids, these males converge onto a bright red coloration (Hill 1992). These patterns suggest that the observed correlation between father and son plumage color reflects the pleiotropic effects of inherited viability or "good genes" (G. E. Hill 1991), rather than the inheritance of alleles that code for different plumage variants directly (also see Hill 1992).

Summary of Case Studies

Although ruffs and queleas are from distantly related taxonomic groups, the similarities in the plumage of these two species are striking (table 2). Despite molting into conspicuous, sexually dimorphic breeding plumages, these plumages are apparently not indicators of quality. We argue that these observed patterns (table 2) are more consistent with the hypothesis that plumage color in these species functions instead as identity signals.

In this study, we compared identity signals with quality signals because quality signaling is currently the most commonly invoked explanation for sexually dimorphic animal ornamentation. Other hypotheses, such as runaway sexual selection (Fisher 1930), sensory exploitation (Kirkpatrick and Ryan 1991), and mate-compatibility signaling (Wedekind 1994), are also important alternative hypotheses for the evolution of ornamentation, but we do not consider them in detail here. Disentangling identity signaling from these other alternatives provides a substantial challenge for future studies. However, an important distinction between identity signals and other types of signals is that identity signals should occur only in species where recognition behavior is particularly important (Whitfield 1987).

Is IR Important in Ruffs and Queleas?

Johnstone (1997) used a game theory model to demonstrate that signalers will be favored to provide individual identity cues when there are sufficient benefits for signalers to receive favorable responses from receivers. In other words, identity signals should be found in species where there is a net benefit to signalers who are recognizable. Are ruffs and queleas such species? Although ruffs lek and queleas are socially monogamous, both species breed under socioecological conditions in which visual cues of identity may be unusually important: stable, high density aggregations formed over a short time period with high rates of male-male interactions (e.g., aggression and territory defense). Under such conditions, being recognizable would be favored by selection on territorial males if IR decreases aggression received from neighbors. Indeed, quelea males tolerate neighbors closer to their nests than they do strangers (Crook 1960; Dale 2000*a*), and ruffs lekking in captivity are more aggressive to neighbors with experimentally altered plumage (D. B. Lank, unpublished data; also see van Rhijn 1991). These observations suggest that aggression is reduced through IR in these species.

In contrast, IR probably does not play as important a role for house finches. During breeding, male house finches are nonterritorial and pursue their reproductive efforts under more dispersed, more densely vegetated conditions (Hill 1993). Indeed, it is generally accepted that plumage coloration in house finches primarily functions as an advertisement of quality (e.g., see Olson and Owens 1998).

Other IR Systems

Other candidate IR systems involving other sensory modalities offer further support for our model. One of the most convincing studies is the work by Beecher and his colleagues on the begging calls in nestling swallows (*Hirundinidae*). In swallows, the young of colonial species have more variable begging calls than do young of noncolonial species. Individual calls are stereotyped and thus would be useful as identity signals. Parents of colonial species are also better at distinguishing their own young from unrelated offspring based on these calls (Stoddard and Beecher 1983; Medvin and Beecher 1986; Loeche et al. 1991; Medvin et al. 1993; also see Leonard et al. 1997). This suggests that offspring that produce distinctive calls have

Table 2: Properties of the breeding plumage coloration in the three study species

Plumage characters	Ruffs	Queleas	House finches
Relative variability	High	High	Low
Frequency distributions	Complex	Bimodal	Unimodal
Condition dependent	No	No	Yes
Correlated with fitness	No	No	Yes
Correlations between characters	No	No	Yes
Genetically determined	Yes	Yes	No

been favored by selection, presumably because they garner a greater portion of their parents' parental care, and that this negatively frequency dependent selection has resulted in increased overall variation in the begging calls (Medvin et al. 1992). Moreover, in strong accordance with our model, Beecher (1982) has shown that, in cliff swallows *Petrochelidon pyrrhonota*, various components of the auditory signals used in recognition vary independently of each other. Furthermore, cross-fostering experiments suggest that variance in cliff swallow begging calls is genetically determined (Medvin et al. 1992).

The dramatic variances in egg coloration in both common murres *Uria aalge* and masked weavers *Ploceus taeniopterus* also appear to be identity signals. Common murres nest on rocky ledges in huge colonies at extremely high density. They lay a single egg, and because no actual nest is built, this egg's position in the colony can change in the chaos of day to day colony life. Murres are able to locate their own eggs after they have been experimentally switched with neighboring eggs. However they tend to make more mistakes when their eggs are switched with eggs that are similarly colored to their own (Tschantz 1959). Similarly, in masked weavers, a female is less likely to reject eggs added to her clutch when they are similar to her own eggs (Jackson 1990). In this species, nests are subject to very high rates of intraspecific nest parasitism, and so variation in eggs may help a female identify correctly her own eggs from parasitic ones (Jackson 1992). Based on our model, we expect that, in both species, parameters of egg coloration will display complex distributions, co-vary independently of each other, and be genetically determined.

Variance in human facial appearance provides another interesting polymorphism that may have been shaped by selection for recognizability. The diversity in human faces offers a rich source of information that is regularly used for identifying individuals. Identity signals in our species could be adaptive for a variety of reasons, such as large group sizes (most human groups include 150 people or more; Ridley 1998) coupled with the importance of status hierarchies, reputations, and widespread delayed reciprocal altruism. If human facial characteristics are identity signals, then they should be composed of genetically determined subcomponents that assort independently and display complex distributions with high variance.

We suggest that IR signaling systems are widespread in nature. In addition to the examples mentioned above, IR has been associated with phenotypic variation in a number of other species, including variation in the appearance of ruddy turnstones *Arenaria interpres* (Whitfield 1986), Harris sparrows *Zonotrichia querula* (Watt 1986), and sand lizards *Lacerta agilis* (Olsson 1994); olfactory variation in scent markings of various species of mammal (Halpin 1980); and acoustical variation in the begging calls of colonial penguin nestlings (Lengagne et al. 1997) and in the vocalizations of neighboring territorial songbirds (Lambrechts and Dhondt 1995) and neighboring territorial fish (Myrberg and Riggio 1985). If these and other signaling systems are composed of traits that have been specifically selected to signal individual identity, then they should exhibit properties similar to those we describe here for ruffs and queleas.

Acknowledgments

We thank G. E. Hill for generously allowing us extensive use of his data on house finches; P. B. Buston, S. T. Emlen, R. Johnstone, J. Poston, P. W. Sherman, A. Sih, E. A. Tibbetts, F. Widemo, and D. Winkler for comments on the manuscript; the Cornell Graduate School and the Exploration Society for support (J.D.); the Malilangwe Conservation Trust and Humani Ranch (Save Conservancy) for permission to work on queleas in Zimbabwe; A. P. Dale, D. J. Dale, R. Hartley, and P. Mundy for help in Zimbabwe; the Natural Sciences and Engineering Research Council of Canada for grants to D.B.L. and F. Cooke; C. Smith for help with the ruff research program; and the National Science Foundation for a grant to H.K.R. This research comprises a portion of J.D.'s doctoral thesis requirements (Cornell University).

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Associate Editor: Andrew Sih

The Auk 118(3):759–765, 2001

Visual Signals for Individual Identification: The Silent "Song" of Ruffs

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Abstract.—Breeding male Ruffs (*Philomachus pugnax*) appear to communicate individual identity through extreme variation in coloration and pattern of their plumages. If plumage variation evolved to provide sufficient information to signal individual identity, we might expect different plumage components to vary independently. We find that variation in four plumage characteristics is largely independent. Previous studies produced conflicting answers about plumage-component independence, perhaps because they failed to separate two genetically distinct behavioral categories of males, which differ in plumage types, in their analysis. We propose that using plumage variation to signal individual identity, rather than voice (used by most other bird species) was favored by lengthy daytime male display in open habitats in close proximity to receivers. However, signaling associated with the unique dimorphism in this species' male mating behavior might also have influenced the evolution of extraordinary plumage diversity in this species.

Breeding male Ruffs (*Philomachus pugnax*) have the most variably colored and patterned feather tracts of any species of nondomesticated bird. This extraordinary variation facilitated study of sexual selection by allowing an early student to follow mating success of individuals at leks using natural markings alone (Selous 1906–1907), and it has long been assumed to function as a cue for individual identity for Ruffs themselves (Hogan-Warburg 1966, van Rhijn 1983, 1991). Individual identification based on plumage variation has been demonstrated experimentally for just a few species of birds (Whitfield 1986, Watt 1986), including Ruffs (experiments by A. Segre Terkel *in* van Rhijn 1991; D. B. Lank et al. unpubl. data). Whereas many species of birds identify individuals by voice (Stoddard 1996, Wiley 2000), male Ruff courtship and aggressive displays are completely silent.

Did plumage variation in Ruffs specifically evolve to facilitate individual variation? Is the functional design of plumage variation consistent with that adaptive hypothesis? Characters specifically evolved to facilitate individual identification should have certain properties (Beecher 1982, Dale 2000, Dale et al. 2001). The most fundamental is sufficient phenotypic variation among individuals to facilitate discrimination by receivers. One simple and powerful way to generate such variation is to have independently varying signal components, each with high variance, that combine to produce many different phenotypes.

We examine to what extent the most prominent plumage characteristics of breeding male Ruffs vary independently. Previous analyses have produced conflicting results (Table 1; van Rhijn 1991). We revisit that question using automated and quantitative measurements of plumage characteristics, and by

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considering whether two behavioral types of male ruffs, which differ in predominant plumage colors, should be analyzed separately.

Background.—Ruff males molt into breeding plumage prior to and during spring migration. Following a prealternate body molt on the wintering grounds (Pearson 1981), adult males grow fluffy ornamental feathers of a neck ''ruff'' and ''head tufts'' during a supplemental molt (Jukema and Piersma 2000) that continues during migration. The ruff, head tuft, and body feathers vary in color and pattern in ways comparable to the pelages of domestic cats (*Felis domesticus*), ranging from white through rusts to blacks (Cramp and Simmons 1983, Hayman et al. 1986), and being solid colored, flecked, barred, and patchy in both regular and irregular arrangements (Glutz von Blotzheim et al. 1975). Males lose their display feathers immediately after the breeding season, typically prior to migration, and complete their prebasic molt after migration (Pearson 1981).

Within days of arrival on the breeding grounds, adult males aggregate at leks located at open sites, often near preferred nesting areas (Andersen 1948, Lank and Smith 1987, Höglund et al. 1998). Most males establish ~0.3 m diameter mating courts, located only 1–2 m apart, which they aggressively defend against most other breeding males. However, males with substantial amounts of white, and little black, in their ruff and head tufts do not attempt to establish mating courts (Hogan-Warburg 1966, van Rhijn 1973). Instead, these ''satellites,'' which comprise 15–20% of males, share display courts with the territorial ''independent'' males (Hogan-Warburg 1966, Hugie and Lank 1997, Widemo 1998). The behavioral difference between territorial and satellite morphs is determined by alternative alleles of a balanced genetic polymorphism (Lank et al. 1995, 1999; Widemo 1998), and plumage differences also appear to have a genetic basis (Lank and Smith unpubl. data).

Lekking males advertise their presence at long distances by flashing their wings or hovering over courts when they detect flying Ruffs (Hogan-Warburg 1966, Widemo and Owens 1995). All other intra- and intersexual display occurs at close quarters on the ground (Hogan-Warburg 1966, van Rhijn 1973, 1991). Females visit multiple courts and multiple leks for about a week prior to egg-laying, mate with one or several males (Lank et al. 1995, in press), and provide all parental care.

Methods.—This analysis is based on photographs of the breeding plumages of 82 male Ruffs caught near Oulu, Finland, in the springs of 1984–1990. The photos were digitized and analyzed with Adobe Photoshop® version 3.0 (Dale 2000). Photographs were taken under ambient outdoor light, and most included a color standard used to ensure colors were consistent among images. We reduced variation between photographs by standardizing the contrast in

TABLE 1. Tests of relationships between plumage characteristics of breeding male Ruffs.

Relationship examined	Source of sample	*n*	Relationship	Reference
Ruff color × head tuft color	Captured on breeding grounds	39	Nonrandom	Andersen 1948
	Museum specimens	164	Nonrandom	Andersen 1948
	Observed on leks	214	Nonrandom	Hogan-Warburg 1966
	Collected on migration	80	Random	Geethe 1953
	Described at leks	100	Random/non[a]	J. Shepard, in Drenekhahn 1975
	Caught at leks	98	Nonrandom	van Rhijn 1991
	Collected on migration	110	Nonrandom	Drenckhahn 1975
	Caught on breeding grounds	77	Random	This study
Ruff color × ruff patterning	Shot, on migration and breeding	508	Random	Lindemann 1951
	Caught at leks	98	Random	van Rhijn 1991
	Caught on breeding grounds	81	Random	This study
Ruff color × head tuft patterning	Caught at leks	98	Nonrandom	van Rhijn 1991
	Caught on breeding grounds	78	Nonrandom	This study
Ruff or head tuft color × wattle color	Caught at leks	98	Random	van Rhijn 1991
	Caught on breeding grounds	62	Random	This study
Ruff pattern and wattle color	Caught on breeding grounds	52	Random	This study

[a] Significance varies depending on color categorization scheme.

each image using the ''Auto Levels'' option under the ''Image: Adjust'' menu in Photoshop®.

We quantified four characteristics of Ruff breeding coloration. (1) *Ruff shade*: to simplify the analysis of ruff coloration, we used Photoshop's® histogram function to reduce color to a grayscale value ranging from black (= 0) to white (= 255). Under that scale, brown is measured as dark grey, whereas shades of rust and buff are lighter grey. We scored only the predominant shade in the ruff when more than one was present. We divided scores by 2.55 to produce a scale ranging from 0 (=black) to 100 (=white). (2) *Head tuft shade*: if several shades were present, we scored the predominant shade at the end of the head tufts. (3) *Wattle hue*: breeding male Ruffs lose feathers on their faces and develop papillae-like facial wattles around their eyes and the base of the bill. Wattles range in hue from deep red to yellow. We used Photoshop's® ''Color Picker'' to quantify that trait. Because all wattle hue values fell between pure red (0) and pure yellow (60), we treated hue as a linear variable, with lower values indicating more red. For convenience, we refer to wattle hue as a ''plumage'' characteristic. (4) *Ruff pattern*: pattern was scored as a categorical variable. We recognized (a) solid, for uniform ruffs, (b) flecked, being sprinkled with small spots, (c) barred, including lines and stripes, and (d) splotchy, including all other irregular secondary ruff markings. Repeated measures of the same males using separate photographs demonstrated that our measures were highly repeatable (ruff shade: $r^2 = 0.97$, $n = 7$; head tuft shade: $r^2 = 0.97$, $n = 5$; wattle hue: $r^2 = 0.72$, $n = 3$, ruff pattern: $r^2 = 1.0$, $n = 6$). Variance in scores for color standards were much lower than variance in actual plumage scores: variance in standards as a percentage of variance in plumage scores were 2.2–13.4% for ruff shade (five standards, $n = 14$ photos), 2.4–4.3% for head tuft shade (five standards, $n = 13$ photos), and 12.4% for wattle hue (one standard, $n = 11$ photos). Not all characteristics were available for all birds.

Males were identified as either independents or satellites on the basis their behavior, where known, or from their plumage type (Hogan-Warburg 1966), which includes more information than the characters included in this paper.

Results.—Both plumage brightness characters had complex multimodal distributions, with high frequencies of predominantly black tracts and a spread across other shades (Fig. 1A, B). The modality of wattle colors was difficult to resolve with that sample (Fig. 1C), but may be uni-, bi,- or even trimodal, with peaks at red, orange, and yellow (c.f. van Rhijn 1991). Patterns were distributed evenly (Fig. 1D), but this could change with the system of categorization.

Plumage brightness was not significantly correlated between ruff and head tuft (Table 2, Fig. 2), indicating that those two characters assort largely independently. Five of the six correlations between characters are not significant (Table 2). Head tuft color covaried with ruff pattern, however, with darker head tufts over represented among birds with flecking and barring. In contrast to earlier studies, we analyzed satellites separately from independents, because satellite plumages cover a narrower range of colors, lacking black tracts. The results are similar when the whole sample or only independents are examined; our sample was insufficient to test satellites only. The unimodal distribution of pattern types among the satellites (solid ruffs only, Fig. 1D) is an artifact of a small sample that does not reflect the full spectrum seen in nature. Finally, the independent males scored with both light ruff and light tufts (upper right corner of Fig. 2) also had patches of black or brown that are not included in this analysis.

Discussion.—Wiley (2000) recently suggested that sexually selected aspects of bird song might be aptly termed auditory ''plumes.'' The display plumages of Ruffs, conversely, function in some ways as a silent ''song.'' The most prominent plumages characteristics of breeding male Ruff demonstrated high variance, non-normal frequency distributions, and varied largely independently of each other. Why did previous studies of covariation produce conflicting results (Table 1; van Rhijn 1991)? Statistical power does not appear to explain the differences. In addition to potential methodological differences in scoring plumage characteristics, a more subtle effect may be differential representation of satellites in samples. Because satellites have a smaller range of colors than independents (Hogan-Warburg 1966; Figs. 1A, B), samples with higher proportions of satellites are more likely to produce significant correlations. Because satellites and independents have different movement patterns, proportions differ among samples collected on migration versus breeding grounds, birds observed at leks versus more widely on the breeding grounds, and even for birds captured versus counted at leks.

The nonindependent patterns we document agree with details of previous studies. Both the significant relationship between head tuft color and patterning of the ruff (Table 2) and a paucity of birds with brown or rusty colored ruffs but white head tufts (Fig. 2) occur in the most comparable previous tabulations (Hogan-Warburg 1966, van Rhijn 1991).

The independent variation of Ruff plumage characters is consistent with the hypothesis that variation evolved specifically to facilitate individual recognition (Beecher 1982, Dale 2000, Dale et al. 2001). A popular alternative functional explanation for plumage variation in other species is that it indicates aspects of a male's condition, or quality (Rohwer 1975, Andersson 1994, Hill and Montgomerie 1994). Signals evolved to identify individuals should not be condition-dependent, and not correlate with fitness (Dale et al. 2001). Evidence against condition-dependence is that despite uniform rearing conditions,

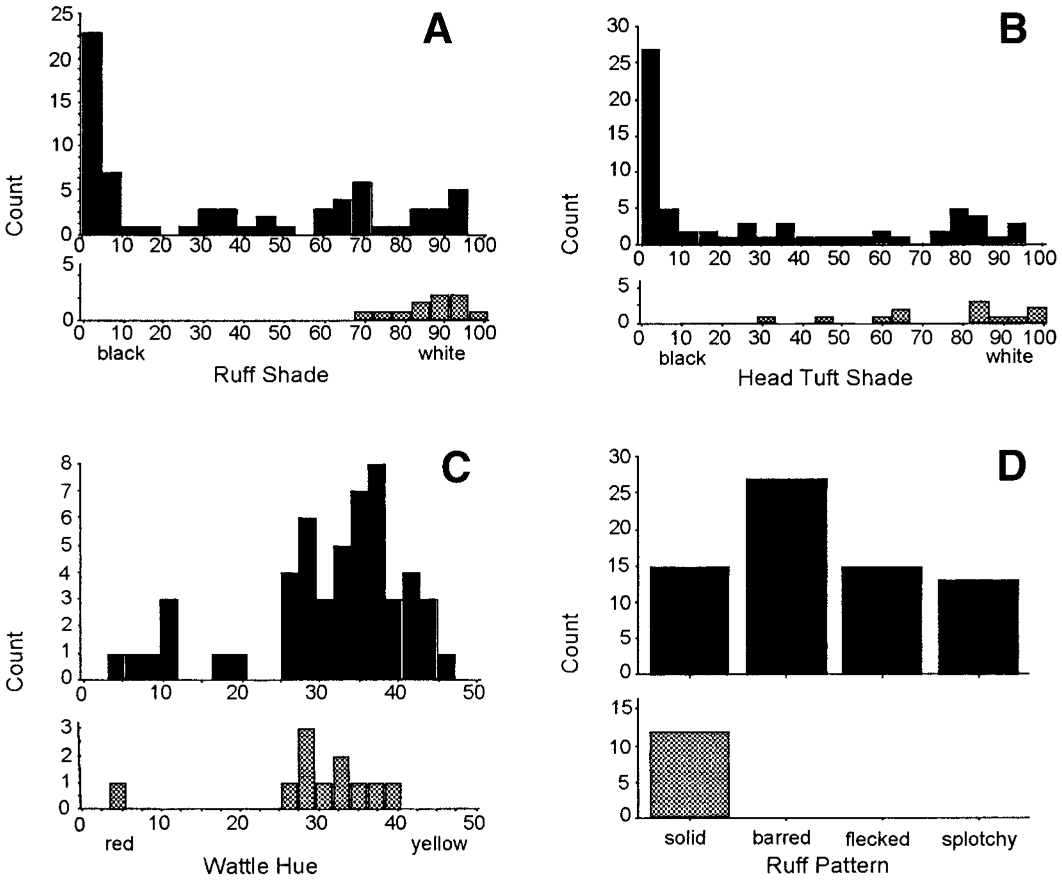

FIG. 1. Frequency distributions of four characters measured in the breeding coloration of male Ruffs (*n* = 82). Separate distributions are shown for residents (black bars) and satellites (grey bars). (A) ruff shade, (B) tuft shade, (C) wattle hue, (D) ruff pattern. See methods for scaling and categorization.

captive-reared populations display the full range of color variation observed in the wild (D. Lank and C. M. Smith unpubl. data). Male Ruffs do have age and condition-dependent characters that do correlate with mating success, including the length and density of display plumes, extent of facial wattles, and leg and bill color, as well as behavioral displays and social interactions (Shepard 1975, Hill 1991, Widemo 1997). In sharp contrast, however, all authors conclude that plumage coloration is not correlated with mating success (Selous 1906–1907, Hogan-Warburg 1966, Shepard 1975, Hill 1991, van Rhijn 1991, D. Lank and C. M. Smith unpubl. data).

Although no formal studies of neighbor–stranger recognition using vocal signals of shorebirds have been published, behavioral observations and song descriptions from numerous species suggest that does occur (e.g. Baker 1982, Miller 1984). Ruddy Turnstones use both variable plumage and calls to signal individual identity (Ferns 1978; Whitfield 1986, 1988, and pers. comm.). Ruffs now use plumage variation, rather than vocal variation, to signal their identity. Why might this change have occured?

The most important features of Ruff breeding biology that may have favored the evolution of visual signals, and made vocal signals of lesser value, are lengthy daytime display in open habitats in close proximity to multiple receivers. Resident males remain on leks throughout the long arctic days (Lank and Smith 1987). Plumage variation allows those males to continuously signal their identity to lekmates and visiting females without incurring the additional costs of vocal signals. Ruff mating courts are only approximately 1–1.5 m apart, and residents and satellites often cooccupy courts, at times in physical contact (Hogan-Warburg 1966, van Rhijn 1991, Hugie and Lank 1997), making it the most densely packed of all lekking birds. At such close quarters, long-distance transmission through visually obscured environments, a major advantage of vocal signals, does not apply.

TABLE 2. Correlations between plumage and wattle characters in male Ruffs. Results of analysis are given for the entire sample of males (upper right matrix) and for the sample with satellites excluded (lower left matrix). Spearman rank correlations were used to evaluate relationship between continuous quantitative characters, and Kruskal-Wallis tests were used to evaluate relationship between pattern (a categorical character) and the quantitative traits. Boldface indicates $P < 0.05$.

	Ruff	Head Tuft	Wattle	Pattern
		(Satellites included)		
Ruff		*Rho* = 0.14	*Rho* = 0.16	H = 5.5
	—	*n* = 77	*n* = 62	*n* = 81
		P = 0.21	*P* = 0.22	*P* = 0.14
Head tuft	*Rho* = −0.16		*Rho* = 0.12	H = 17.6
	n = 65	—	*n* = 62	*n* = 78
	P = .19		*P* = 0.33	***P* = .0005**
Wattle	*Rho* = 0.26	*Rho* = 0.16		H = 5.2
	n = 51	*n* = 51	—	*n* = 63
	P = 0.07	*P* = 0.27		*P* = 0.16
Pattern	H = 1.9	H = 12.2	H = 4.8	
	n = 69	*n* = 66	*n* = 52	—
	P = 0.59	***P* = .007**	*P* = 0.19	
		(Satellites excluded)		

Silence on the lek is not entirely restricted to Ruffs. Several other species with ground-displaying males use little vocalization once females are on mating courts. Buff-breasted Sandpipers (*Tryngites subruficollis*), a close relative of the Ruff, in which males defend moderately sized, clumped-lek territories, have nearly silent close-range courtship (Lanctot and Laredo 1994). Despite their notorious long-distance calls, courting peafowl (*Pavo cristatus*) do not vocalize in that situation.

The unique male behavioral dimorphism in that species (Hogan-Warburg 1966) may also have contributed to the evolution of extreme plumage differentiation among male Ruffs. Plumage differences might have initially evolved to signal a male's probable behaviour as a satellite or independent. Given the complex relationship between the two types of males (van Rhijn 1973, 1991; Hugie and Lank 1997, Widemo 1998), selection favors a reliable indicator of male type. The most honest signal would covary genetically with alleles for male behavioural morph (Lank et al. 1995, 1999), and a plumage marker might have evolved to serve that purpose. Once males of different colors became acceptable mating partners, directional selection on female preferences for plumage color per se would have been relaxed, allowing spread of additional mutations, if signaling individual identity were favored (Johnstone 1997).

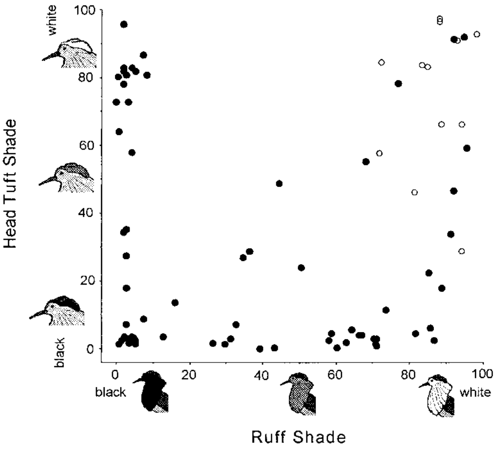

FIG. 2. Scattergram of ruff shade vs. head tuft shade. Independents are closed circles and satellites are open circles.

Acknowledgments.—We thank Connie Smith for participating in the field work, and P. Whitfield, F. Widemo, and D. Kroodsma for comments on the manuscript. This research was funded by grants to D.B.L. from the National Geographic Society, the Fulbright Foundation, the National Science Foundation and the NSERC. J. D. was supported by the Cornell University Graduate School.

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Received 4 August 2000, accepted 2 February 2001.
Associate Editor: D. Kroodsma

CHAPTER SEVEN:

Future Directions

Introduction

Like most research, the results that I have presented in this thesis raise many more questions than they can begin to answer. In this final chapter, I briefly outline what I feel are some of the more important issues that need to be addressed in future studies of red-billed quelea plumage; and more generally, individual identity signaling

1) Queleas

In chapter 4, I demonstrate that quelea males are able to discriminate neighboring males from unfamiliar males. However, whether or not males actually use variation in plumage to help them with this discrimination is unknown. This question needs to be addressed. I attempted to answer this question in three different ways. First I manipulated male plumage in the wild to see if neighboring males would respond aggressively to males who appear different than what they are used to. Unfortunately this strategy is rather ineffective because male queleas invariably desert their nests after they have been trapped at them. Secondly, I tried manipulations in captivity; but these experiments were largely unsuccessful because my captive flocks were small and the males were all very familiar with each other, the breeding attempts in the captive flocks were limited and unsynchronized, and the aggression rate in the captive flocks was comparatively low compared to rates of males during the nest-building phases of a colony. Finally, I also tried to address this question using habituation experiments of pairs of males kept in small cages. This did not work at all as the males did not behave normally in the small cages.

There are two additional methods that could potentially be used to address whether males use plumage traits for recognition decisions. First, one could use mounts in the field (e.g. see Whitfield 1986). Depending on whether males respond normally to realistic mounts of queleas placed near their nests, this technique could provide a powerful way to evaluate potential recognition cues. A second approach would be to set up groups of unfamiliar males, and then measure whether possessing unique plumage patterns results in lower degrees of aggression received during dominance hierarchy formation (Watts 1986; also see below). I hope to be able to perform these experiments sometime in the very near future, but would encourage anyone else to investigate these questions as well.

Additional questions about quelea recognition concern the specific fitness advantages associated with recognizability in this species. In previous chapters I have argued that 'dear-enemy' or neighbour-stranger recognition is the important factor. Thus males who are recognizable are predicted to be harassed less by neighbors during territory formation, and to gain fitness advantages as a result. This hypothesis needs to be tested rigorously. Furthermore, in chapter 4 , I described how quelea males treat strangers more aggressively than neighbors. Exactly why are strangers a bigger threat than neighbours? Finally, what role does mate recognition play in the evolution of recognizability in red-billed queleas? It could be an important, even critical, factor.

2) Socio-ecological correlates to recognizability: a comparative approach

In Chapter 4, I ask why individual recognition might be important for ruffs and queleas. We argue that since both species breed in high-density aggregations with high rates of social interactions (e.g. aggression and territory defense), individual recognition based on visual cues may be unusually important. Clearly this question needs to be addressed more rigorously. Moreover this question only scratches the surface of many more general issues about individual identity signalling. Specifically: 1) How common is identity signaling in the animal kingdom? 2) What socio-ecological parameters are they associated with? And 3) what are the advantages and disadvantages of signaling identity through sound, sight, or smell? One might be able to gain insight into these questions through the application of the comparative method. For example, across different bird species, does the degree of plumage variability correlate with any environmental parameters that should be associated with increased need for recognition (e.g. group size, degree of breeding synchrony, or density)? To my knowledge, no such studies have been conducted. However, early work on swallow nestling begging calls by Beecher and his colleagues (see Chapter 4) have demonstrated the potential power of such an approach. In swallows, nestling call variability is much higher in species who nest in large colonies where parents could potentially confuse their own offspring with the many other nestlings in the colony (Medvin et al. 1993)

3) The fitness benefits of being recognizable.

The fundamental assumption of the identity-signalling hypothesis is that individuals who have rare signal phenotypes (more recognizable) experience a selective advantage over individuals who have common signal phenotypes (less recognizable). To my knowledge no one has demonstrated a benefit to being recognizable, although indirect evidence suggests that such benefits might be widespread (Watt 1986; Rohwer and Roskaft 1989). In my view, the experimental demonstration of a fitness benefit being associated with signaling individual identity will be extremely important, and will have major implications to the fields of behavioral ecology and animal communication.

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