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

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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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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

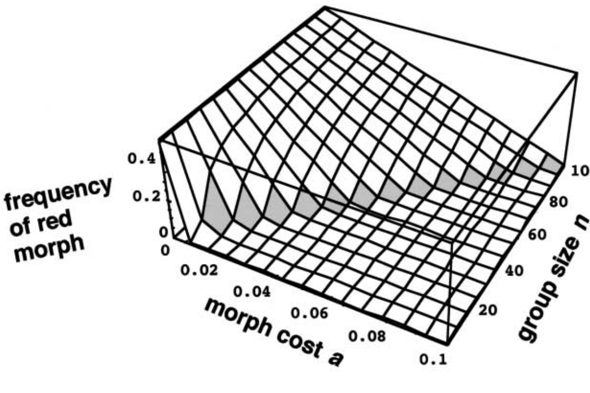

**Figure 1:** Equilibrium frequency of the red morph as a function of the morph cost ($a$) and the number of group members $n$; $c = 0.001$.

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

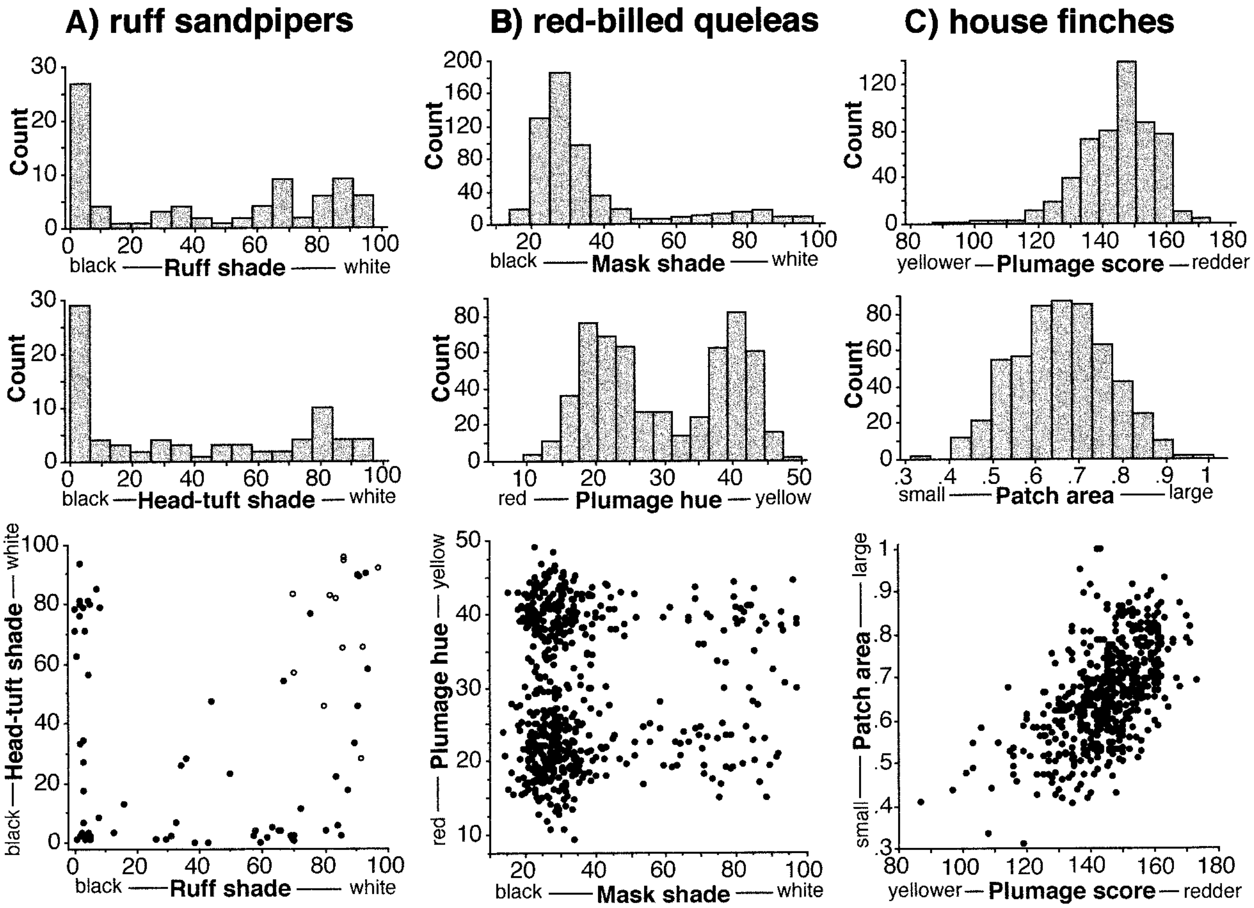

Figure 2: Comparison of plumage characters in the three study species. *A*, Ruff sandpipers; data on 77 wild males (65 independents, *filled circles*, and 12 satellites, *open circles*) caught near Oulu, Finland, from Lank and Dale (in press). *Upper panel*, frequency distribution of ruff shade; *middle 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.

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