# 2

# Intraspecific Variation in Coloration

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With some birds, it seems that if you've seen one, you've seen them all. American Crows (*Corvus brachyrhynchos*), for instance, appear remarkably similar from individual to individual: jet black from bill to tail. There is undoubtedly some degree of variability among individuals (especially from the perspective of a crow), but variation in crow patterning and blackness is unarguably low. Why are crows so uniformly black?

At the other extreme, breeding male Ruffs (*Philomachus pugnax*) are among the most variably colored wild species of bird. Ruffs display impressive ornamental plumes around their necks and heads that range in color from white, cream, straw, rust, brown, to black. These plumes are often multicolored, with secondary colors appearing in diverse patterns (e.g., bands, bars, flecks, spots, splotches). The legs, bills, and facial wattles of male Ruffs also vary from yellow, orange, red, green, to black (Plate 7). All of these traits, which for the most part vary independently of one another (Lank and Dale 2001), make each Ruff appear unique. Why are Ruffs so variable?

More generally, why are there such striking differences in the degree to which coloration is variable within species? In this chapter, I suggest that most intraspecific color variation (Box 2.1) can be understood from a framework based on communication theory, in which "signalers" use coloration to provide information to "receivers" (Wiley 1983; Krebs and Davies 1993; Johnstone 1997a). To understand color variability in this context, we therefore need to resolve the specific information that birds broadcast about themselves with color.

## Box 2.1. Properties of Intraspecific Color Variation

Studying variability in color is challenging, because coloration varies in so many different dimensions. First, the actual color itself can vary along the tristimulus color variables of hue, saturation (or chroma), and brightness (HSB; see Chapters 2 and 3, Volume 1). Second, a patch of color can vary in its size and/or pattern. Third, there can be variability in the number of different patches of color (or traits).

Often intraspecific color variability involves alternative appearances among different groups of *classes* of individuals within a species (Butcher and Rohwer 1989). For example, males often look different than females. Four basic groups of classes of individuals that differ in coloration can occur within a species: (1) age groups (e.g., delayed plumage maturation), (2) sexes (sexual dichromatism), (3) seasonally different populations (seasonal variation), and (4) geographically different populations (geographical variation).

Once the color dimension of interest has been identified and this dimension has been measured in a sample of individuals, there are three basic properties of variability that can be considered: (1) the degree of variability can range from low to high, (2) the modality of variability can be unimodal or multimodal, and (3) the continuity of variability can be continuous or discrete (Figure B2.1). Across different species, these properties vary substantially, and this is the case whether one is looking at variability within (intra-) or between (inter-) different classes.

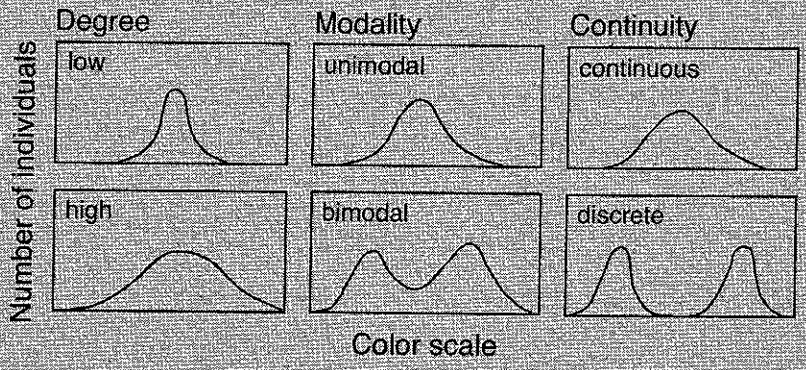

Figure B2.1. Three basic properties of color variability in birds.

*Table 2.1.* Seven Different Types of Information That Can Be Signaled by Avian Coloration

| Signal type | Selection | Signaling contexts | Comment |
|---|---|---|---|
| Quality | | | |
| Indicators | Directional | Mate-choice, competition, parent-offspring, predation | Condition dependent, differentially costly |
| Amplifiers | Stabilizing | Associated with indicators | Reduce perception error of indicator variation by receivers |
| Attractiveness (Fisher traits) | Directional | Mate-choice | Not required to be costly, but can be if signal elaboration is extreme |
| Strategy | | | Strategy-dependent cooperation required |
| Gender | Disruptive | Sex recognition | |
| Status-related | Disruptive | Delayed-plumage maturation, condition-dependent strategies | |
| Mating | Disruptive | Cooperative display, territorial versus parental strategies | |
| Genetic compatibility | | | Signals compatibility alleles for any loci for which there are multiple optimal combinations |
| Reinforcement | Disruptive | Mate choice—avoid fitness-reducing hybridization | |
| Species recognition | Stabilizing | Mate choice—avoid interspecies breeding | |
| Within-population | Diversifying | Mate choice—MHC signaling, increase offspring heterozygosity | |
| Kinship | Negative frequency dependent | Cooperation, inbreeding avoidance | Recognition of unfamiliar kin, recognition template based on receiver's own phenotype, or phenotype of known kin |
| Individual identity | Negative frequency dependent | Neighbor-stranger, kin and mate recognition, dominance hierarchies, reciprocal altruism | Recognition of familiar individuals, receiver recognition template based on signaler's phenotype |
| Presence | | | |
| Honest (beacons) | Stabilizing | Mate attraction, distraction displays, flocking, startle-displays | Signal contrasts with ambient light conditions |
| Dishonest (camouflage) | Stabilizing | Avoid detection by predators or prey | Signal blends with ambient light conditions |
| Dishonest (apostatic) | Negative frequency dependent | Avoid detection by predators or prey | Avoidance-image hypothesis |

Typically, studies of communication focus on receivers of signals. They ask: Do receivers respond to signal variation? If so, why? In this chapter, however, I focus on the signaler. If a signaler has been selected to broadcast particular information using color (either honestly or dishonestly), then what is the outcome of such selection in terms of signal properties? In other words, what do signals that reveal (or conceal) different kinds of information look like?

For color to reveal specific information, there have to be mechanisms whereby that information is coupled with specific expressions of color. Thus I consider both the information content of signal variability and the potential sources of that variability. All variability ultimately arises from two sources: genes and the environment. Genetic variation comes from genes that code directly for different color variants, or alternatively through genes that have pleiotropic effects on color development. Environmental variability arises through an interaction among various environmental parameters (e.g., social environment, parasites, territory quality, age, season, nutrition; Chapter 12, Volume 1) and the penetrance of genes coding for signal phenotypes.

Birds use color to communicate information in at least seven broad categories: quality, attractiveness, strategy, genetic compatibility, kinship, individual identity, and presence (Table 2.1). I develop predictions about the nature of variability for each of these seven kinds of signals, under the assumption that color variation is directly related to variation in the specific information revealed.

Table 2.1 summarizes the seven kinds of color-based signals that I discuss in this chapter, the nature of selection acting on the signals (e.g., stabilizing versus directional), and the signaling contexts expected to be associated with these signals. Table 2.2 summarizes the expected patterns of variability of color-based signals that function to reveal these types of information. Below, I review these signals, their relevant selective forces, expected forms of variability, and observed patterns in selected case studies. Although my focus is on visual signals in birds, the generalizations developed here should offer insight into signal properties in all sensory modalities in all taxa.

## Quality

Most recent research on bird colors has focused on their potential function as condition-dependent signals of quality (or "indicators")—cues that communicate information about aspects of the bearer's relative phenotypic and genetic constitution (Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Grafen 1990; Andersson 1994; Olson and Owens 1998; Dale

*Table 2.2.* Color-Based Signal Types in Birds and Their Expected Properties of Signal Variability, Differences among Classes, and Degrees of Genetic or Environmental Determination

| Signal type | Degree of variability | Modality of variability | Continuity of variability | Interclass variability[a] | Source of variability |
|---|---|---|---|---|---|
| Quality | | | | | |
| Indicators | Moderate | Unimodal | Continuous | Age, sex, season, geographic | Environmentally determined and pleiotropic effects of additive genetic variance for condition, signal alleles fixed |
| Amplifiers | Low | Unimodal | Continuous | | Genetically fixed |
| Attractiveness (Fisher trait) | Low | Unimodal | Continuous | Sex, geographic | Genetically determined, degree of genetic variance depends on equilibrium state |
| Strategy | | | | | |
| Gender | High (between strategies)<br>Low (within strategies) | Bimodal | Discrete | Sex[b] | Genetically determined, sex-dependent |
| Status-related | High (between strategies)<br>Low (within strategies) | Bimodal (assuming two strategies) | Discrete | Age, sex | Environmentally determined, age dependent |
| Mating | High (between strategies)<br>Low (within strategies) | Bimodal (assuming two strategies) | Discrete | Sex | Genetically determined |
| Genetic compatibility | | | | | |
| Reinforcement | High between, low within | Bimodal (unimodal within) | Discrete | Sex, geographic | Genetically determined |
| Species recognition | Low | Unimodal | Continuous | Sex | Genetically determined, fixed |
| Within-population composition | Moderate | Multimodal | Continuous | Sex | Genetically determined |
| Kinship | Moderate | Multimodal | Continuous | Sex | Genetically determined, polygenic |
| Individual identity | Moderate to high | Multimodal | Continuous | Sex | Genetically determined, polygenic |

| | | | | | |
|---|---|---|---|---|---|
| Presence | | | | | |
| Honest (beacons) | Low | Unimodal | Continuous | Sex | Genetically determined, low additive variance |
| Dishonest (camouflage) | Low, (high if ambient conditions variable) | Unimodal (multimodal if ambient conditions variable) | Continuous (Discrete if ambient conditions vary discretely) | Sex, season, geographic | Genetically determined, low additive variance (high variance if ambient conditions variable) |
| Dishonest (apostatic) | Moderate to high | Multimodal | Discrete | None | Genetically determined, high additive variance |

a. Possible (but not required) interclass variation resulting from differential selection on classes to broadcast particular information types.

b. Required.

et al. 2001). Here I consider quality to be a broad concept that includes various aspects of a bird's constitution (e.g., social status, parental care abilities, "good genes"). All quality indicators share in common the requirement of high and differential costs to their bearers for the signals to be reliable (Zahavi 1975; Kodric-Brown and Brown 1984; Grafen 1990). All three of the major mechanisms of color production in birds (carotenoids, melanins, and microstructures) have been demonstrated to be related to various aspects of individual quality (Chapter 12, Volume 1; Chapter 6; also see Figure 2.2). Even the presumably cheapest color to develop, white (no pigmentation), is related to quality in some species (Jones 1990; Pärt and Qvarnstrom 1997; Török et al. 2003). Currently there is a great deal of interest devoted to resolving the specific costs of color displays and the specific aspects of quality they reveal.

### Degrees of Variability

Signals of quality have higher degrees of variability than nonsignaling morphological traits (Alatalo et al. 1988; Møller and Hoglund 1991; Møller and Pomiankowski 1993; Andersson 1994; Pomiankowski and Møller 1995; Cuervo and Møller 1999, 2001; Dale et al. 2001). However, our understanding of the nature of this variability in quality signals is rudimentary. Honesty in quality signals would break down if individuals did not vary in their ability to meet the theoretically required costs of signal elaboration (Zahavi 1975; Kodric-Brown and Brown 1984; Grafen 1990); without variation in the relative costs, receivers would not be favored to pay attention to the signals (Alatalo et al. 1988; Andersson 1994; Dale et al. 2001).

High variability in quality signals is a product of the complex developmental processes involved in their expression. First, quality signals are strongly environmentally dependent. Indeed, aspects of the social environment (Griffith et al. 1999; Parker et al. 2002; McGraw et al. 2003), parasite exposure (McGraw and Hill 2000), nutritional conditions (McGraw et al. 2002), exposure to pollution (Eeva et al. 1998), and global climatic conditions (Garant et al. 2004) have all been shown to affect expression of quality signals. Second, quality signals express high degrees of additive genetic variance (Pomiankowski and Møller 1995), based on pleiotropic effects of genes affecting condition (Rowe and Houle 1996; Kotiaho et al. 2001). At equilibrium, the genetic basis for the signal traits themselves is expected to be fixed (Maynard Smith 1985; Andersson 1986; Kirkpatrick 1986; Pomiankowski 1987, 1988; Tomlinson 1988; Heywood 1989; Hill 1994), and all individuals in a population are expected to have similar "potential" to produce elaborate (costly) signals (Hill 1992, 1994). How individuals fulfill that potential (i.e., the degree of penetrance of the fixed signal genes) is influenced by a large number of pathways that independently contribute to trait expression, resulting in high phenotypic variability (Rowe and Houle 1996; Kotiaho et al. 2001).

There are obvious differences across species in the extent to which color-based quality signals vary, although this variability has not yet been quantified (see Box 2.2). For example, carotenoid-based plumage redness signals male quality in both House Finches (*Carpodacus mexicanus;* Plate 14; Hill 1991) and Northern Cardinals (*Cardinalis cardinalis;* Plate 25; Wolfenbarger 1999). Yet apparent intraspecific variability in plumage hue and saturation of male cardinals is considerably lower than it is in House Finches (Figure 2.1). Why do cardinals vary less than House Finches? One possibility is that carotenoids are more limiting in House Finches, perhaps due to an exclusively granivorous diet (Hill 1993), and so lower carotenoid availability is manifested in higher overall signal variability. In addition, as the color of quality signals approaches full expression, overall variability is expected to be lower, as directional selection compresses the trait against physical limitations of expression. Thus, as the mean saturation level gets higher, smaller differences in saturation might be more differentially costly than they are in less saturated species.

In general, a coherent theoretical framework for understanding why there are differences among species in the variability of quality signals is badly needed, as is a comprehensive descriptive survey of overall patterns of variance in colorful signals of quality in birds. All we know so far is that quality signals tend to be variable (indeed, high variability in a signal is often argued as supportive of quality signaling; Box 2.2). Exactly why quality signals vary and why some vary much more than others is poorly understood.

## Frequency Distributions

Quality is a quantitative trait affected by various environmental and genetic factors. Because quantitative traits generally demonstrate unimodal distributions, aspects of quality, and the signals that reflect them, are also expected to be unimodal (Dale et al. 2001). Indeed, analysis of putative color-based quality signals in most species typically reveals unimodal frequency distributions (Figure 2.2; also see Senar 1999; Dale et al. 2001; Ripoll et al. 2004).

The only known exception to unimodal frequency distributions for colorful quality signals occurs in the bimodal distribution of badge size in Eurasian

## Box 2.2. Quantifying Color Variability

Typically, biological comparisons of variability involve calculating coefficients of variation (CV) for traits of interest (i.e., the standard deviation as a percentage of the mean). Studies demonstrating high CV for sexually selected traits (e.g., tail length in widowbirds; Alatalo et al. 1988) in comparison to morphological traits thought to be under stabilizing natural selection (e.g., tarsus length) form the empirical basis for the commonly accepted idea that sexually selected traits tend to be highly variable (Alatalo et al. 1988; Cuervo and Møller 2001). In general, sexually selected traits demonstrate CV on the order of 10–20%, whereas naturally selected traits demonstrate CV ranging from 2% to 5%.

The use of CV to compare color variability is not possible, because the dimensions of color are often assigned along arbitrary numerical scales. Thus variance in color variables does not usually scale with the mean, and so the CV of a color variable is not directly comparable to the CV of a length measurement. Indeed, studies that have used the high CVs of color-based traits as empirical support for signaling functions are statistically flawed (e.g., McGraw and Hill 2000; Massaro et al. 2003; Mennill et al. 2003; McGraw 2004; Doucet et al. 2005).

For example, consider variation in color brightness, a scale that ranges from 0 (no reflectance) to 100% (full reflectance). If two samples have mean brightness values of 10 and 90, and each sample has a standard deviation of 10, the CV of the two samples will be 100% and 11%, respectively. These values suggest the first sample is nine times more variable than the second. However, the opposite conclusion would be drawn if the brightness scale is redefined into an equivalent "darkness" scale that ranges from 0% (no absorption) to 100% (full absorption).

CV calculated using hue values on the 360° color wheel (e.g., Massaro et al. 2003) are even more problematic, because the numerical value for any given hue is completely arbitrary (e.g., a mean hue of 359° is very similar in appearance to a mean hue of 1°, both red, because pure red is defined as hue = 0°). Consider variability in bill versus plumage hue in Red-billed Queleas (see Figure 2.9). Bill hue is strikingly less variable than plumage hue in this species, but CVs for bill and plumage are similar (29.03% and 34.82%, respectively), simply because red is assigned lower hue values than yellow.

CV calculated on hue values from reflectance curves (e.g., peak wavelength; Doucet and Montgomerie 2003; Mennill et al. 2003; Shawkey et al. 2003) are also problematic. Equivalent variability in longer wavelength radiation (yellow and red light) will automatically generate lower CVs than shorter wavelength radiation (blue and ultraviolet light). These CVs are not biologically meaningful, because red does not appear "longer" than blue.

I strongly recommend using standard deviations (SDs) alone (or interquartile range) to compare color variability for measurements of HSB. For example, in Red-billed Queleas, SDs for bill and plumage hue are 1.64 and 10.01, respectively, demonstrating that bill hue is indeed much less variable. When the range of hue values brackets 0, negative hue values (e.g., hue = −1° instead of 359°) could be used to calculate SD, or alternatively, circular statistics could be used to calculate indices of variance. Comparisons of variability between different color dimensions (e.g., SD in hue versus SD in saturation) should be avoided. Particular caution is required when comparing SD in hue, because as mean brightness and saturation decrease, equivalent variances in hue measures result in decreased degrees of perceivable color variability (e.g., see Figure 2.7). Ideally, comparisons of color variability should thus incorporate comparisons of areas or volumes occupied by the observed scatter along saturation versus hue plots (e.g., see Figure 2.1), or saturation versus brightness versus hue plots, respectively. For color variables based on reflectance spectra, statistical techniques that quantify differences in the shapes of reflectance curves need to be developed to quantify and compare variability among species and traits.

Meaningful comparison of color variability to morphological character variability under natural selection, such as tarsus length (e.g., Massaro et al. 2003; Mennill et al. 2003), is not possible. However, comparisons between color traits thought to be sexually selected versus color traits thought to be naturally selected could potentially lead to important insights. Indeed, these kinds of comparisons are badly needed to truly evaluate if sexually selected coloration is more variable than naturally selected coloration, as expected by current theory.

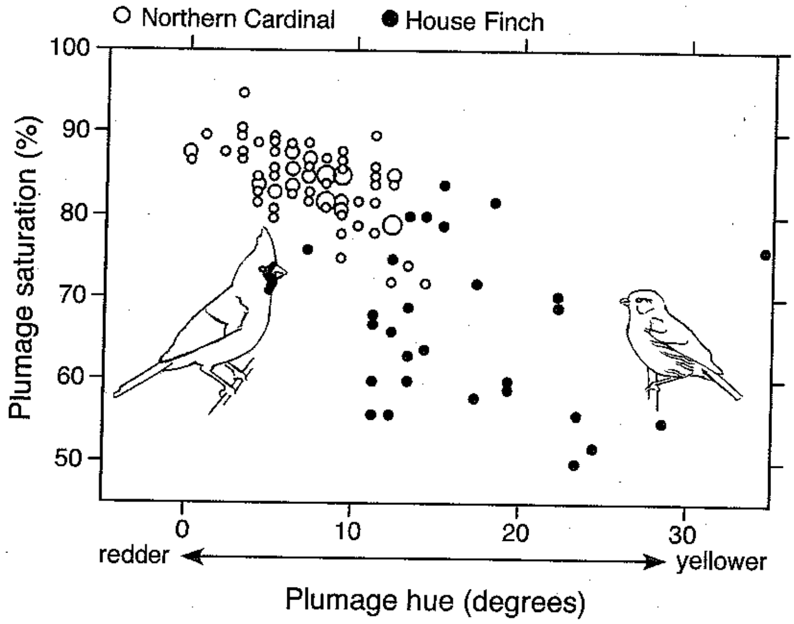

Figure 2.1. Saturation versus hue for red plumage in male Northern Cardinals ($n = 80$) and House Finches ($n = 28$). Apparent variability (amount of scatter) in plumage redness is lower in cardinals than in House Finches. Color scores were measured at the center of the breast on museum specimens at the Cornell University Vertebrate Collection (Ithaca, NY) using methodology described in Dale (2000).

Siskins (*Carduelis spinus;* Senar et al. 1993; Ripoll et al. 2004; Chapter 2; Figure 2.2; Plate 12), a trait that signals status. Rohwer and Ewald (1981) argued that bimodal distributions could be stable for status signals, provided they are maintained by negative frequency-dependent selection. A stable bimodal distribution can result if individuals of different dominance ranks play mutually beneficial roles (Rohwer and Ewald 1981; also see Ripoll et al. 2004; Chapter 3). In such cases, badge size, in addition to being a signal of quality (status), also signals a variable behavioral strategy. Bimodality then results from disruptive selection for honest strategy signaling (see the section on strategy below), as opposed to continuous and unimodal frequency distributions expected when there is directional selection on quality and the signals that reveal it.

## Amplifiers

Recently there has been increased interest in the hypothesis that signal traits function as quality amplifiers (Hasson 1991; Brooks 1996; Taylor et al. 2000). Amplifiers do not reveal quality per se, but instead reduce perceptual errors by

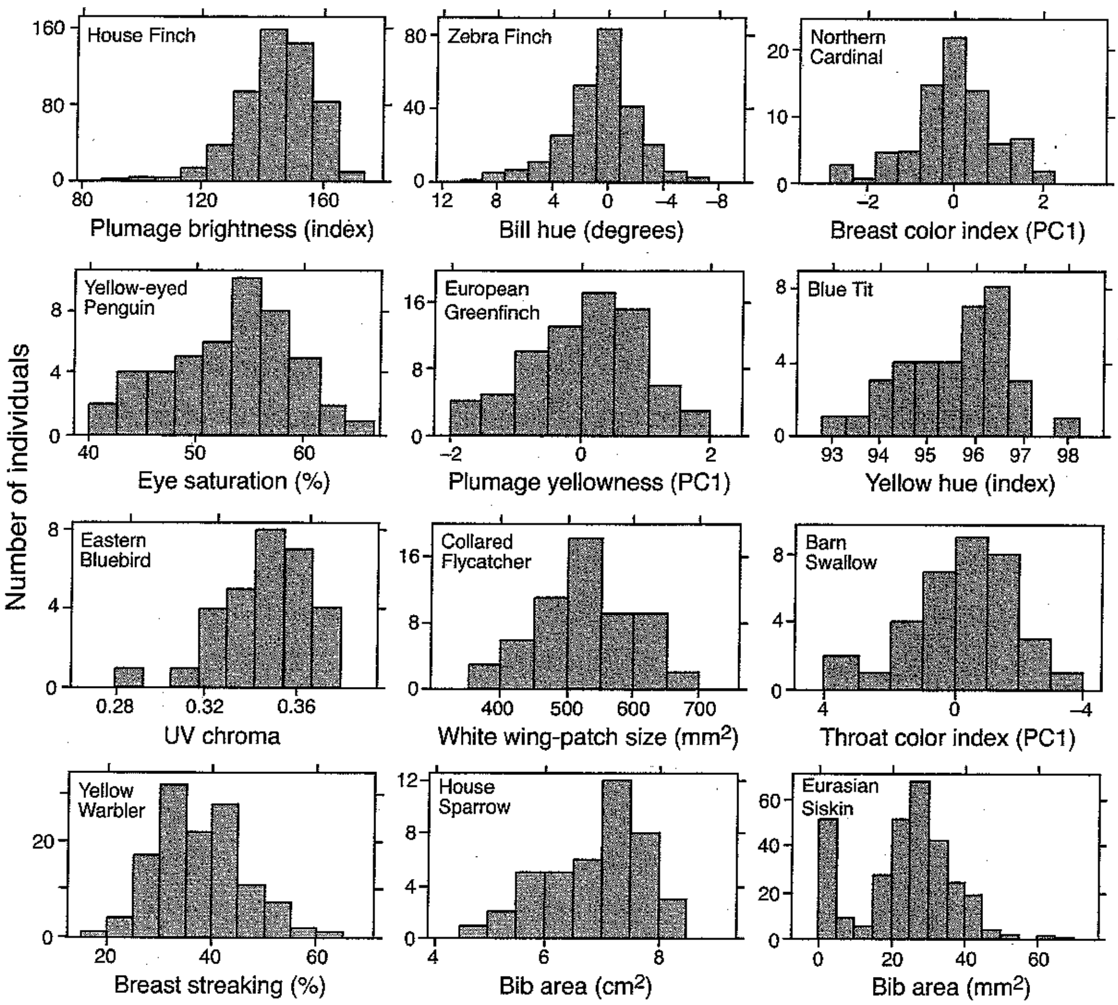

Figure 2.2. Frequency distributions of color-based quality indicators in 12 bird species. Graphs are arranged such that color expression associated with higher quality occurs toward the right. Note the unimodal, normal, or approximately normal distribution of color expression for a range of color types including carotenoid, structural, white, phaeomelanin, and eumelanin. Adapted or redrawn from Hill (1992), J. Dale and T. D. Williams (unpubl. data), J. Dale (unpubl. data), Massaro et al. (2003), Merila and Sheldon (1999), Senar et al. (2002), Siefferman and Hill (unpubl. data), Török et al. (2003), Safran and McGraw (2004), Yezerinac and Weatherhead (1997), McGraw et al. (2003), and Senar et al. (1993).

receivers with respect to evaluating other traits that do signal quality (Hasson 1991). With color-based signals, amplifiers can be considered as portable "color standards" attached to quality signals, which help receivers accurately gauge true variance in a quality signal by comparing the quality signal with the amplifier. Because amplifiers are expected to result in tighter correlations between actual quality and apparent (perceived) variability in the "amplified" quality signal, they can be considered as a form of noncostly quality signaling.

Color-based amplifiers can initially spread in a population as a form of male cheating. Noncostly traits that enhance the apparent expression of a color display will be favored and spread to fixation (Hasson 1991; Hill 1994; Taylor et al. 2000). Once all signalers have the amplifying trait, however, receivers can actually get a more reliable perception of variance in the quality signal (Brooks 1996). At equilibrium, amplifiers are therefore expected to express relatively low unimodally distributed variability and to be fixed, genetically determined traits unrelated to signaler condition (i.e., to be noncostly). In particular, black coloration may often be the best color amplifier because black offers a strong contrasting background for other bright colors.

Many species with bright yellow or red patches that signal quality tend to have jet black borders that could function as amplifiers. McGraw and Hill (2000) noted that, in American Goldfinches (*Carduelis tristis;* Plate 30, Volume 1), cap blackness was not particularly variable and does not appear to be condition dependent. Experimentally diseased goldfinches showed no changes in the expression of their black caps, although they suffered significantly reduced expression of carotenoid-based yellow plumage. Because the cap borders yellow feathers, but is not itself related to quality, these authors speculated that black caps might function as amplifiers.

Similarly, many birds have iridescent and glossy plumage (with a strong ultraviolet [UV] component) that is underlain with apparently uniform and fully melanized feathers. Such full melanization would provide a constant, and therefore noninterfering, background to UV reflectance, by absorbing the flanking regions of the spectrum and making the UV signal appear more saturated. In an aviary experiment, calorie restriction reduced the saturation of glossy blue-black dorsal plumage in male Brown-headed Cowbirds (*Molothrus ater;* McGraw et al. 2002; Plate 7, Volume 1), suggesting that iridescence was condition dependent. In contrast, melanization of the adjacent brown hood of the cowbirds was not affected (McGraw et al. 2002), implying that melanization may generally be more resilient to variability in the physical environment (also see Hill and Brawner 1998; McGraw and Hill 2000). In cowbirds and many other species, uniform melanization may therefore function as an amplifier of iridescent and glossy plumage.

## Attractiveness

Models of runaway sexual selection (Fisher 1930; Lande 1981; O'Donald 1983; review in Andersson 1994) assume that genes for the expression of traits (expressed in males) and genes for mating preferences for those traits (expressed in females) become genetically correlated through assortative mating. Thereafter, trait genes and preference genes can co-evolve into extreme forms through a self-reinforcing positive feedback process. Runaway traits, or "Fisherian traits," are therefore arbitrary signals of attractiveness. They are arbitrary because runaway selection can act on any traits with perceivable genetically determined phenotypic variance and an associated preference, and they are not expected to be related to male condition.

How much variability should a color-based Fisherian trait express? Runaway selection can continue exaggerating traits until (1) all genetic variability is exhausted and either the trait or preference genes, or both, become fixed or (2) increased natural selection against extreme versions of the traits (or preferences) halts the runaway process. In the case of color-based Fisherian traits, physical constraints for color expression offer an obvious wall to halt phenotypic elaboration (i.e., saturation and brightness have limits beyond which further elaboration is impossible). Therefore Fisherian traits should display relatively low degrees of intrapopulation variance, provided population-level genetic variance in traits becomes fixed (Alatalo et al. 1988)—especially if strong directional sexual selection tends to run colors into full expression over evolutionary time.

Alatalo et al. (1988) argued that runaway selection predicts high variance between different geographic locations, provided there are limitations to gene flow between populations and that the populations each arrive at different equilibrium states. Therefore runaway traits are expected to express high degrees of geographic variability (Alatalo et al. 1988). Indeed, runaway selection models suggest that the process can result in explosive speciation events within taxa with intense sexual selection, as traits and preferences in different ancestral populations diverge (Iwasa and Pomiankowski 1995; Pomiankowski and Iwasa 1998). Thus runaway traits are expected to express low degrees of intrapopulation variability (see above), but high degrees of interpopulation and interspecies variability.

Interspecific diversity in plumage coloration in taxa with highly polygynous species, such as birds of paradise (Paradisaeidae), pheasants (Phasianidae) and manakins (Pipridae) (Anderson 1994; Prum 1997) provides promising candidates for signals that evolved through runaway sexual selection. Male coloration across different species in these taxa is extremely diverse, whereas female coloration tends to be rather uniform interspecifically. Indeed, Prum's (1997) detailed study of manakins offers compelling support for the importance of

Fisherian processes in the evolution of plumage ornamentation. When compared with closely related and monogamous tyrant flycatchers (Tyrannidae), the diversity of manakin traits suggests that manakin coloration has evolved by an explosive and unconstrained evolutionary mechanism not consistent with predictions based on quality-indicating mechanisms.

If male coloration in manakins and other predominantly lekking taxa are the products of runaway selection, then intraspecific variability in these species is expected to be relatively low, unimodally distributed, geographically variable, and unrelated to male quality. These predictions have not been specifically tested, but Kodric-Brown and Brown (1984) noted that apparent intraspecific variability in manakin coloration appears to be particularly low.

### Strategy

Different individuals within a species often pursue alternative strategies (Rohwer and Ewald 1981; Gross 1996). When individuals form strategy-dependent cooperative alliances, signalers can be selected to broadcast information that honestly reveals their strategy, provided that it facilitates mutually fitness-enhancing interactions among strategy types (cooperation is considered here in the broadest sense of an ultimately mutualistic relationship, even if competitive elements remain between cooperators). Variability in coloration could therefore function to communicate strategy-related information (Rohwer and Ewald 1981). Strategy signals are expected to display bimodal and discrete distributions (assuming two nonoverlapping alternative strategies). Furthermore, variation in strategy signals is expected to be more strongly genetically determined when the strategy is fixed (e.g., Lank et al. 1995), but more strongly environmentally determined when the strategy is conditional (e.g., Greene et al. 2000).

## Signals of Gender: Sex Recognition

Males and females represent the two fundamental alternative reproductive strategies, typically maintained at an equilibrium frequency close to 50:50 through negative frequency-dependent selection (Fisher 1930). Males and females obviously need to cooperate to successfully reproduce, so they must effectively communicate their sex. Sexually dichromatic traits, therefore, could function in sex recognition (Noble and Vogt 1935; Noble 1936).

Visually based, specially evolved signals of gender should occur in species for which additional gender-revealing cues (i.e., sex-specific traits selected for

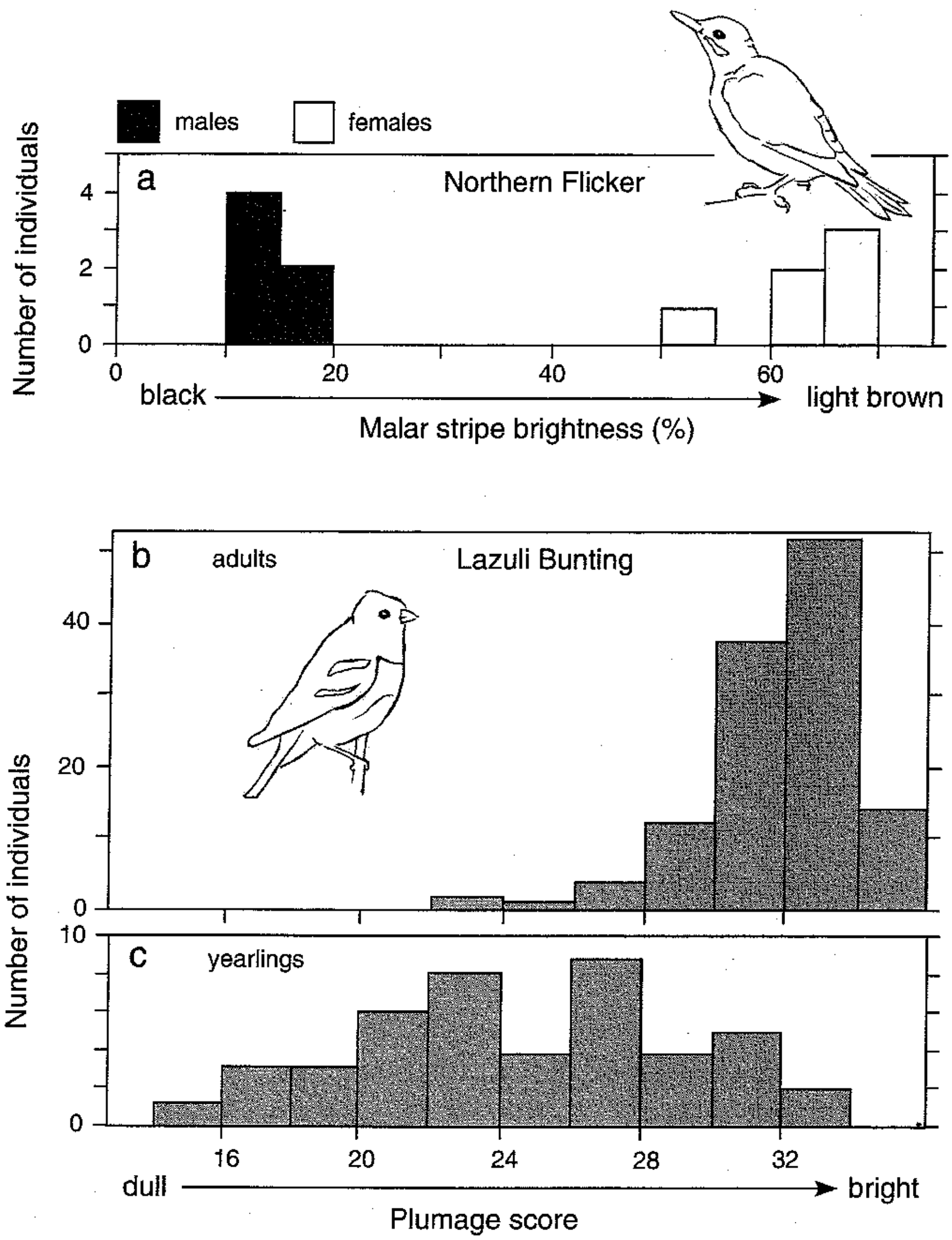

Figure 2.3. Frequency distributions of plumage color are bimodal, as expected for strategy signals, in (a) both male and female Northern Flickers and (b) adult and (c) yearling Lazuli Buntings (redrawn from Greene et al. 2000). Data on flickers were collected from museum specimens at the Cowan Vertebrate Collection at the University of British Columbia (Vancouver, BC) using methodology described in McGraw et al. (2003).

by other processes) are less apparent. Presumably, signals of gender would not need to be particularly conspicuous, are expected to demonstrate completely distinct distributions between the sexes, and are expected to vary little within each sex (Figure 2.3a). Gender signaling is thus expected in species whose genders have very similar roles during courtship and reproduction (because such species are less likely to reveal gender through other cues) and in species that are sexually monomorphic in appearance (apart from the gender signal).

Woodpeckers (Picidae) often have highly conspicuous coloration patterns, but usually there is one small difference between males and females (Short 1982; Moore 1987). Noble (1936) demonstrated that a female Northern Flicker (*Colaptes auratus*) was treated aggressively by her mate when experimentally given a black mustache streak typical of a male (see Figure 2.3a).

The potential for visual signals of gender to play a role in reducing wasted mating effort has been demonstrated, paradoxically, in a sexually monochromatic species lacking obvious plumage variation between the sexes (Langmore and Bennett 1999). In Long-tailed Finches (*Poephila acuticauda*), plumage color scores in males and females overlap considerably, as demonstrated by detailed spectrophotometric analysis. Males were equally likely to court and copulate with both unfamiliar males and unfamiliar females. Langmore and Bennett (1999) argued that this species is monochromatic to allow individuals the opportunity to strategically conceal their gender to reduce sexual competition (Burley 1981).

## Signals of Status-Related Strategies

Plumage variability can often reveal aspects of quality related to social status (see Chapter 3 and the section on quality above). Although quality signals are generally expected to be unimodally distributed, bimodal frequency distributions could arise if individuals of different statuses pursue different behavioral strategies (Rohwer and Ewald 1981). For example, status-related strategy signaling may provide a general explanation for patterns of delayed plumage maturation (DPM) (Chapter 3), wherein individuals in different age-groups have diagnostic color patterns. Indeed, many instances of DPM appear related to status signaling (Lyon and Montgomerie 1986), with subadult plumages reflecting subordinate status and adults being less aggressive to individuals in subadult plumage.

DPM should be considered strategy signaling whenever individuals from different plumage types pursue alternative strategies involving mutually fitness-enhancing interactions among strategy types. For example, in socially monogamous, territorial species, adult males with subadult neighbors can enhance their reproductive success through extra-pair fertilizations (EPFs) gained in the nests of subadult males (Morton et al. 1990; Perreault et al. 1997; Richardson and Burke 1999; Greene et al. 2000). Honest signals of subadult status could reveal a strategy wherein younger individuals concede EPFs to adult neighbors in exchange for reduced territorial aggression from them, thereby increasing the subadults' potential to acquire high-quality territories, as has been specifically argued for Lazuli Buntings (*Passerina amoena;* Greene et al. 2000). Thus bimodal distributions of plumage variability within a sample of all individuals is expected, and unimodally distributed variability is expected within each strategy type. Lazuli Buntings contrast with this general expectation, however, because yearling plumage color overlaps considerably with adult plumage color (Figure 2.3b,c). However, this exception appears to support the general expectation of nonoverlapping signals between strategies, because yearlings with bright plumage appear to successfully pursue the strategy typically adopted by adults, whereas yearlings with dull plumage (which is never expressed in adults; Figure 2.3b,c) are also able to successfully rear offspring through apparent mutually fitness-enhancing collaborative alliances with adult neighbors (Greene et al. 2000).

## Signals of Breeding Strategy

Individuals often pursue alternative strategies independent of age, status, or gender. An instance of honest strategy signaling occurs in White-throated Sparrows (*Zonotrichia albicollis*), in which adults use plumage color to advertise, independently of sex, a genetically determined variable breeding tactic: territorial versus parental (reviewed in Tuttle 2003). Breeding tactic in these sparrows is associated with a bimodal distribution in plumage color: tan individuals are more parental and white individuals are more territorial (Atkinson and Ralph 1980; Figure 2.4a). As predicted for such a signal of strategy, pairs who mate disassortatively by strategy do much better, strongly suggesting a benefit associated with revealing their reproductive strategy honestly (Falls and Kopachena 1994).

Male Ruffs also have color-based signals of breeding strategy that are genetically determined (van Rhijn 1991; Lank et al. 1995). Resident males (~85% of males) form territories on leks and display to females. Satellite males (~15%) do not defend territories, but instead form cooperative alliances with resident males for mutual display. Many residents allow satellites on their territory, and both males gain copulations from females (van Rhijn 1991). On average, territories with both types of male are more attractive to females than territories with only resident males (Hugie and Lank 1997; Widemo 1998). By signaling their strategies reliably, males could gain fitness through facilitation

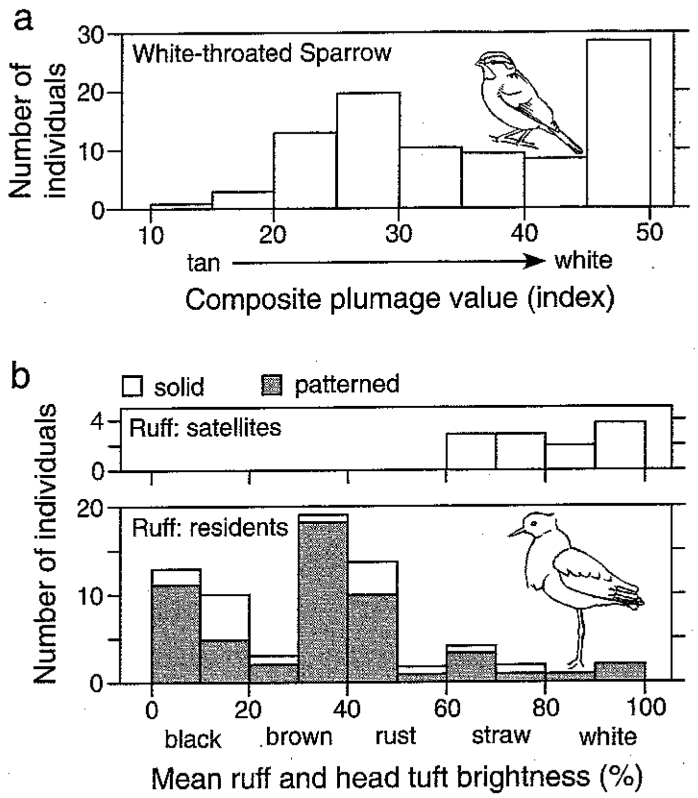

Figure 2.4. Frequency distributions of plumage morphs in (a) White-throated Sparrows (redrawn from Atkinson and Ralph 1980), and (b) Ruffs (adapted from Lank and Dale 2001). Variation in plumage coloration in both species is bimodally distributed, as expected for mating strategy signals. White-throated Sparrow coloration may actually be more distinct between strategy types than is shown in this figure, as Atkinson and Ralph (1980) measured composite coloration in a variety of plumage traits. Plumage color in Ruffs was measured along a brightness scale, which correlates strongly with the variety of different colors found in a population.

of these mutually fitness-enhancing cooperative displays. Indeed, satellites do not look like residents (van Rhijn 1991). They typically have very white and uniform ruffs and very light head tufts, and this plumage type does not overlap to any appreciable degree with the diverse plumage types expressed by residents (van Rhjin 1991; Lank and Dale 2001; Figure 2.4b; Plate 7).

## Compatibility

Recently there has been considerable interest in the hypothesis that individuals actively choose mates with whom they are genetically most compatible (Tregenza and Wedell 2000; Freeman-Gallant et al. 2003; Servedio and Noor

2003; Mays and Hill 2004). Bird coloration could function as signals for such genetic compatibility if it revealed variability in the relevant loci. Compatibility signals are genetically determined traits whose phenotype predicts whether an individual carries particular alleles at any loci for which there are various optimal genetic combinations in a population of potential mating partners.

How does selection maintain positive correlations between genes related to signals and genes that have alleles that are differentially compatible? Selection for reliable signals of compatibility increases with (1) the potential for matings among incompatible genotypes, (2) any reduced opportunity for multiple mating by signalers (thereby reducing selection for signalers to cheat; Wedekind 1994), and (3) strong and ongoing selection against offspring from parents with incompatible genotypes at particular loci (Servedio and Noor 2003), because strong selection maintains high linkage disequilibrium between signal and compatibility alleles.

## Genetic Compatibility among Populations

Color signals related to genetic compatibility might be expected most often during the reinforcement processes of speciation (Dobzhansky 1940; Marshall et al. 2002; Servedio and Noor 2003). When locally adapted populations, subspecies, or closely related sister species overlap in geographic distribution and any hybrid offspring have reduced fitness, selection can favor traits that inhibit interbreeding (Servedio and Noor 2003). Under such conditions, any individual choosing a mate when both genotypes (taxa) are available will face a bimodal distribution of genetic compatibility among potential partners. Signals of taxon identity are thus expected to have bimodal distributions wherever the taxa are sympatric.

Reproductive character displacement is a signature of this reinforcement process (Howard 1993; Sætre et al. 1997; Servedio and Noor 2003). Such character displacement occurs when taxa demonstrate more differentiated characteristics in zones of sympatry than they do in zones of allopatry. Signals of taxon identity are therefore expected to demonstrate high geographic variability. Specifically, within taxa, color variability should be lower and more differentiated in sympatry (where it is under strong selection) than it is in allopatry (where it is under weak selection; Figure 2.5a).

Taxon reinforcement of signals requires that there is (1) selection against hybrids, (2) character displacement in sympatric populations, and (3) assortative mating arising from character displacement in the zone of sympatry

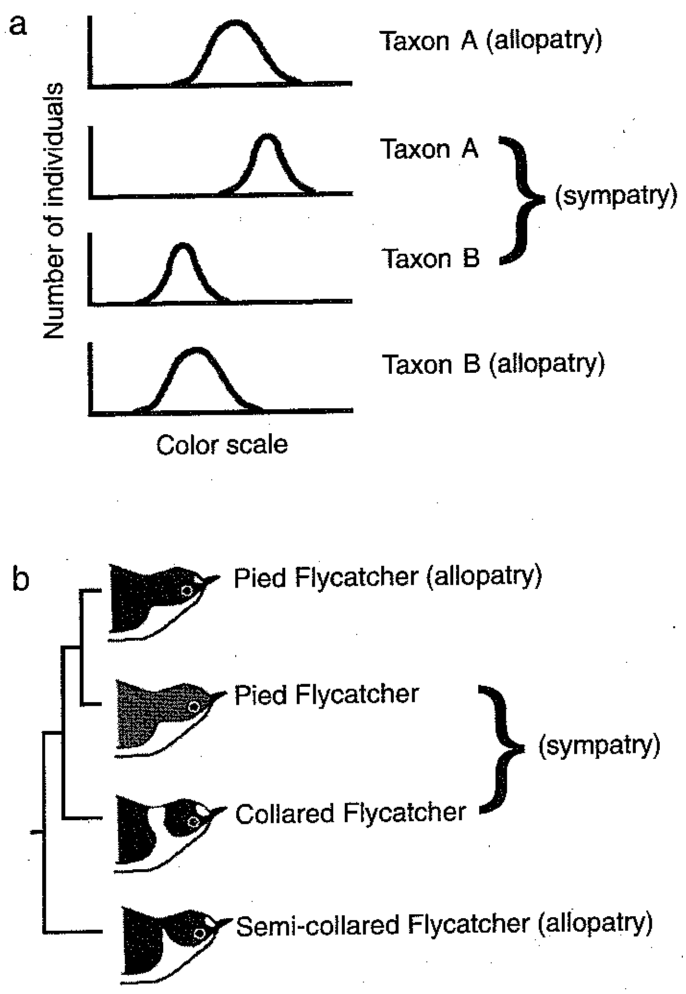

Figure 2.5. Plumage variability and reinforcement. (a) Expected properties of variation in plumage characteristics that function at decreasing hybridization between genetically distinct taxa. (b) Plumage coloration in *Ficedula* flycatchers mapped onto a molecular phylogeny (adapted from Sætre et al. 1997). Populations of Pied Flycatchers occurring in sympatry with Collared Flycatchers have recently diverged in plumage color, increasing the degree of assortative mating within each taxon.

(Sætre et al. 1997). Such conditions appear to occur in *Ficedula* flycatchers. In areas of sympatry, the closely related Collared (*Ficedula albicollis;* Plate 18) and Pied (*F. hypoleuca;* Plate 27, Volume 1) Flycatchers occasionally interbreed. However, hybrid offspring have considerably reduced fitness and, in sympatry, plumage coloration is much more differentiated than in allopatry (Figure 2.5b). Furthermore, females have displaced mate preferences for plumage coloration in areas of sympatry, which results in increased assortative mating (Sætre et al. 1997).

## Species Recognition

When reinforcement processes lead to complete assortative mating between genetically differentiated populations (distinct enough such that no viable offspring are produced during hybridization), then the association between respective signal genes and each species' genome can be considered fixed. In such situations, signal traits might function as species recognition signals: the ultimate compatibility signals. Historically, the concept of species recognition (Wallace 1889; Fisher 1930; Mayr 1963) has received widespread interest as an explanation for interspecific variability in bird coloration (Andersson 1994, McNaught and Owens 2002). However, to date there has been little empirical support for the idea that species recognition has been a strong selective force in the evolution of the broad patterns of avian coloration. McNaught and Owens (2002) tested the species recognition hypothesis using a comparative approach applied to plumage coloration in various Australian species. Contrary to predictions based on species recognition, they found no evidence that sympatric pairs of species were more divergent in coloration than allopatric pairs. McNaught and Owens (2002) concluded that the species isolation hypothesis may be best suited to explain plumage diversity only in very closely related sister taxa for which frequent hybridization is a current and strong possibility.

If species recognition signals do exist in bird colors, what are their expected characteristics? Under the assumption that any signal variation away from the species' mean value would be selected against through increased recognition errors by receivers (i.e., strong stabilizing selection), then signals of species identity are expected to be fixed, genetically determined traits that demonstrate low degrees of unimodally distributed variability. In addition, such signals need not be particularly conspicuous (or costly), as receivers will only be realistically required to differentiate among a limited number of species similar to themselves. Species identity signals are therefore unlikely to explain fully the most conspicuous secondary sex traits, such as highly ornamental coloration (Andersson 1994).

## Genetic Compatibility within Populations

Mate choice that is sensitive to genetic compatibility is also expected to occur *within* populations. However, variable coloration probably provides a poor medium for reliable signaling of intrapopulational genetic compatibility. First, there are no simple mechanisms to couple variability in color alleles with variability in compatibility alleles. Second, with respect to condition-dependent (i.e., costly) plumage coloration, compatibility signaling is unlikely because females cannot use the same color traits to select for mates with overall high-quality genotypes as well as for individual-specific compatibility (Mays and Hill 2004).

One of the most common forms of mate choice for compatibility within populations occurs when females favor partners who are compatible with respect to genetic parasite resistance (e.g., disassortative mating for major histocompatibility complex [MHC] allelic composition; Wedekind 1994; Freeman-Gallant et al. 2003). However, all of the empirical support for MHC-driven mate choice comes from olfactory cues (Egid and Brown 1994; Wedekind and Füri 1997; Tregenza and Wedell 2000). Olfactory cues can be tightly linked to MHC composition because polymorphic MHC loci can create detectable odors via the highly variable glycoproteins they encode by (1) breakdown of the glycoproteins themselves into small evaporating molecules, and/or (2) determination of the specificity of odor-causing bacterial flora that inhabit an individual (Wedekind 1994; Tregenza and Wedell 2000). In strong contrast, there is no intrinsic mechanism whereby variance in plumage alleles will be necessarily coupled to allelic composition of MHC loci. Therefore, unless there is particularly strong and ongoing selection against nonoptimal MHC combinations (which would maintain high linkage disequilibrium between signal and MHC alleles), color cues are an unreliable medium for broadcasting MHC genotypes.

Another form of mate choice for compatibility within populations occurs when individuals prefer mates who have optimal degrees of overall genetic similarity (Bateson 1983; Tregenza and Wedell 2000; Mays and Hill 2004). A signal of overall genetic similarity must be based on multiple polymorphic loci scattered throughout the functional genome (e.g., see Dawkins 1982; Sherman 1991; Sherman et al. 1997). However, the reliability of such signals as predictors of compatibility alleles will eventually deteriorate as signal alleles become independent of alleles at other loci through genetic shuffling at meiotic recombination. At equilibrium, such signals can only reflect similarity with respect to the genetic basis to signal variability, not to the rest of the genome, and are therefore unstable. However, if individuals frequently encounter unfamiliar genetic relatives as potential mates (e.g., through limited dispersal in both sexes), then color variability can reliably signal (shared) genetic similarity. This reliability comes about because, even in distant relatives, recombination will not have had sufficient opportunity to break up linkage disequilibrium between signal alleles and other parts of the genome. In such cases, shared signal alleles between receivers and signalers will predict genetic similarity at many other loci shared through common descent (i.e., linkage disequilibrium is higher in kin; Dawkins 1982). However, such signals can be considered signals of kinship, which I discuss next.

## Kinship

Kin recognition in birds can often be accomplished via the learning of distinctive characteristics of likely genetic relatives that have been identified using other cues, such as positional information (e.g., a nestling's presence in an adult's nest can be a good predictor of kinship). An alternative form of kin recognition occurs, however, when individuals discriminate unfamiliar kin (Dawkins 1982; Sherman et al. 1997). Correctly recognizing unfamiliar kin could increase fitness if receivers behave altruistically to the signaler (Sherman et al. 1997; Petrie et al. 1999). In addition, recognition of unfamiliar kin could facilitate inbreeding avoidance by revealing degrees of overall genetic similarity resulting from shared genetic descent (Sherman et al. 1997; Tregenza and Wedell 2000; Blomqvist et al. 2002; see the section on compatibility above).

Signals of kinship are expected to be variable, genetically determined phenotypes based on multiple polymorphic loci scattered throughout the functional genome (Dawkins 1982; Sherman 1991; Sherman et al. 1997). Receivers could gauge genetic similarity of unfamiliar signalers by comparing the signal to a cognitive template based on their own phenotypes or the phenotypes of known close relatives (Burley and Bartels 1990; Sherman et al. 1997). Signals of kinship should not be particularly costly or conspicuous, but variability needs to be high enough for receivers to easily discriminate phenotypic differences related to kinship.

Recognition of unfamiliar kin may be of widespread importance in avian social interactions (Höglund et al. 1999; Petrie et al. 1999; Shorey et al. 2000; Bloomqvist et al. 2002). For example, Peacocks (*Pavo cristatus*) 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 choosing a lek to join based on some sort of phenotypic variation among males that they used to ascertain potential relatedness. It is unclear, however, whether the cues were color-based or based on another signaling modality, such as sound.

In Zebra Finches (*Taeniopygia guttata*), variability in plumage coloration provides a promising candidate for a visually based signal of kinship. Unfamiliar individuals were found to preferentially associate with relatives (Burley et al. 1990), and it appears as though they could use plumage cues, at least in part, to do so (Burley and Bartels 1990). Zebra Finch plumage is characterized by a variety of high contrasting lines and banding, the variability of which appears to be genetically determined (Burley and Bartels 1990). Plumage variability in Zebra Finches might therefore provide suitable variability for kin recognition, as has similarly been proposed for variability in chimpanzee and human facial features (Parr and de Wall 1990; DeBruine 2004).

## Individual Identity

The use of color variability for individual recognition appears to be widespread. When individuals interact repeatedly, selection can favor the production of identity cues that facilitate individual recognition (Beecher 1989; Johnstone 1997b; Dale et al. 2001). The defining property of a signal of identity (and the difference between an identity signal and a kinship signal) is that the receiver's recognition template (Sherman et al. 1997) is based on the phenotype of the individual signaler. Once learned by receivers, signals of identity can be coupled with additional information, such as territorial residency (neighbor-stranger or "dear enemy" recognition; Wilson 1975), reliability in altruistic interactions (i.e., reputations; Nowak and Sigmund 1998), dominance (Barnard and Burk 1979), mate identity, or kin identity (see Whitfield 1987; Dale et al. 2001 for reviews).

### Properties of Identity Signals

In identity signaling, rare morphs are at a selective advantage because rare varieties are assumed to be more easily recognized than common varieties (i.e., less likely to be confused with other individuals). This negative frequency-dependent selection increases phenotypic variability, and so identity signals are expected to be highly variable. Dale et al. (2001) developed the idea of negative frequency-dependence on identity signals to make specific predictions regarding the expected properties of such traits. In addition to expressing relatively high variability, identity signals are expected to express five other properties. First, they should have polymodal frequency distributions, because negative frequency-dependent selection is well known to maintain phenotypic variability and polymorphisms (Maynard Smith 1982). Second, they should be relatively cheap and not condition dependent, because phenotypes that are distinct but cheap will spread to a higher equilibrium frequency. Third, different signal variants should have equal fitness at equilibrium, because rare phenotypes will spread until all traits have equal fitness. Fourth, they should exhibit an independent assortment of component characters (Beecher 1982; Dale et al. 2001), because correlated traits have a reduced potential for being distinct. Finally, they should occur as fixed phenotypes with high degrees of genetic determination, because receivers can force reliable identity signaling by using inflexible characters for their recognition decisions (which tend toward strong genetic determination). Moreover, if polymorphic loci for signaling traits are located on separate chromosomes, then the theoretically favored low correlations between component traits will be automatically generated by independent assortment of chromosomes at meiosis (Dale et al. 2001).

## Candidate Identity Signals

Plumage coloration in Red-billed Queleas (*Quelea quelea*) provides a promising candidate for a visually based signal of individual identity in birds (Dale 2000, 2001; Dale et al. 2001). The ornamental breeding plumage coloration of male queleas is remarkably variable (Ward 1966; Plate 6). It has the following properties consistent with identity signaling: (1) high variability; (2) complex frequency distributions, at least for some traits; (3) independent assortment of component characters; (4) no condition dependence; (5) no relation to reproductive success; and (6) no age/experience-related variation. In queleas, males breeding in colonies live in a social environment where being recognizable is likely critical—because cohesive social groups (neighborhoods of nesting males) frequently interact within a huge assemblage of unfamiliar individuals (Crook 1960; Dale 2001).

Ruffs have the most variably colorful breeding plumages of any wild bird (van Rhijn 1991; Lank and Dale 2001; Plate 7). Lekking Ruffs are highly territorial, have frequent agonistic interactions with other males, and do not vocalize. Individual recognition between males on leks is obvious (van Rhjin 1991). In the absence of vocal communication, the only likely available recognition cue for Ruffs is plumage variability (Lank and Dale 2001). As in queleas, properties of plumage variability in Ruffs conform well to the expected properties of identity signals (Dale et al. 2001).

## Box 2.3. Testing Identity Signaling

An important but inconclusive test of identity signaling is that color is used for recognition decisions. Because selection can favor receivers that recognize individuals independently of whether signalers benefit from being recognized (Johnstone 1997b; Dale et al. 2001), the demonstration that coloration is used in recognition processes (e.g., Whitfield 1986; also see Tibbetts 2002) does not provide conclusive evidence that the phenotype of the signaler evolved to signal identity.

The critical test centers around the fundamental assumption of the identity-signaling hypothesis—individuals who have rare signal phenotypes (more recognizable) must experience a selective advantage over those who have the most common signal phenotypes (and thus are less recognizable individually). To my knowledge, such a selective advantage has yet to be shown for any putative identity signal in any communication medium in any taxon. Attempts to demonstrate the benefits associated with recognizability should thus be an important focus for future studies of individual recognition. Indirect evidence suggests that such benefits might be widespread (Watt 1986; Rohwer and Røskaft 1989; also see Höjesjö et al. 1998). For example, Watt (1986) argued that decreased aggression observed among more variably plumaged groups of Harris' Sparrows (*Zonotrichia querula*) was consistent with the hypothesis that increased individual recognition within groups facilitated the formation of stable dominance hierarchies. Furthermore, Rohwer and Røskaft (1989) speculated that Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) with manipulated plumage (Plate 10) were better at maintaining their territories than unmanipulated birds, because they were more easily remembered by rivals as good fighters.

Comparative studies offer great potential to provide insight into identity signaling. Early work on begging by swallow nestlings demonstrated the potential power of such an approach (Medvin et al. 1993). In swallows (Hirundinidae), variability in nestling calls is higher in species that nest in large colonies where parents could potentially confuse their own offspring with the many other nestlings in the colony (Medvin et al. 1993; also see Leonard et al. 1997). Furthermore, egg color variability tends to be higher in species with high degrees of brood parasitism, indicating strongly that variability can be increased through selection favoring traits that improve a female's ability to discriminate her own eggs from foreign eggs (Soler and Møller 1996). Whitfield (1987) pointed out how a general comparative approach needs to be applied to avian plumage color variability and individual recognition. Almost 20 years later, this is still the case.

Falconiformes (e.g., hawks and falcons) are among the most variably colored orders of birds (Rohwer and Paulson 1987; Galeotti et al. 2003). Many species are highly territorial, staking large open territories over their hunting grounds, and visual signals of identity could function to reduce needless aggression among neighboring residents and also facilitate mate and kin recognition. Indeed, individual recognition is obvious in diurnal raptors, even at great distances (Tinbergen 1958). Plumage variability in raptors appears, in general, to be strongly genetically determined, typically melanin-based (i.e., presumably cheap), and often multimodal (Rohwer and Paulson 1987)—patterns consistent with identity signaling. Individual identity signaling has not been considered for color variability in raptors, despite a relatively large amount of research devoted to resolving its function. If plumage in birds of prey evolved primarily to facilitate individual recognition, then variability should correlate positively with increased territorial interactions, increased frequency of visual contact among individuals, and increased territory size. In species with sexual differences in the degree of color variability (Fowlie and Kruger 2003), the sex involved in territorial defense is expected to be more variable.

Additional identity signaling systems include highly variable plumage coloration in Ruddy Turnstones (*Arenaria interpres*). In his pioneering study, Whitfield (1986) demonstrated that turnstone color variation is used for neighbor-stranger recognition (but see Box 2.3). Nestling Cliff Swallows (*Petrochelidon pyrrhonota*) have highly variable plumage patterns on their heads (Plate 9) that parents may use to identify their offspring in fledgling flocks (Stoddard and Beecher 1983). Similarly, nestling color in Royal Terns (*Sterna maxima;* Buckley and Buckley 1970), and Red-legged Shags (*Phalacrocorax guimardi;* Rasmussen 1988) is also quite variable and has been argued to be associated with the need for parents to identify young from large non-kin groups of nestlings. In Royal Terns, the observed frequency distributions of nestling coloration in a large sample of chicks offer strong support for the expected

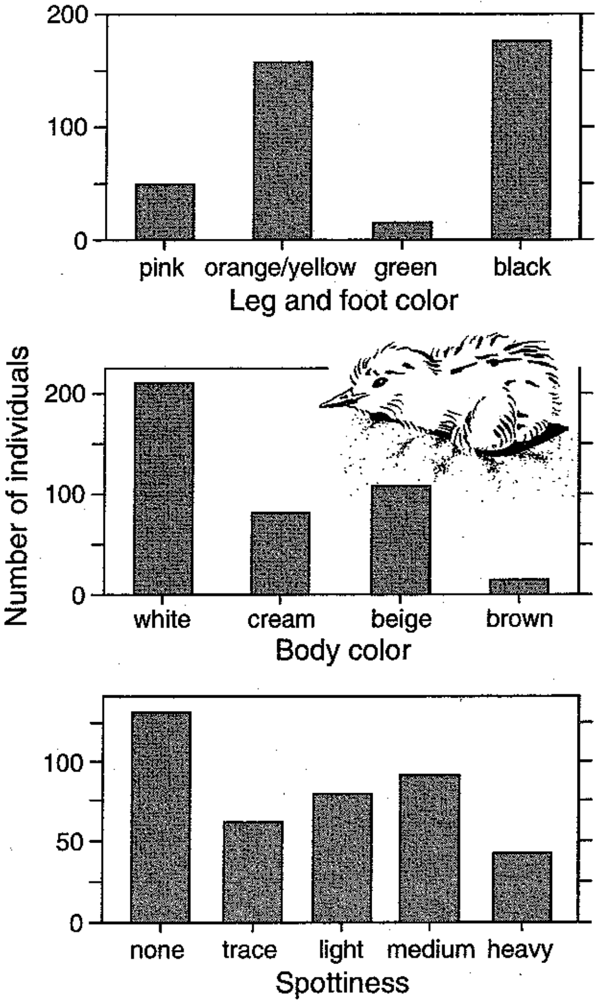

Figure 2.6. Frequency distributions of color traits in Royal Tern chicks ($n$ = 400) demonstrate complex patterns, as expected for identity signals. Adapted from Buckley and Buckley (1970).

complex frequency distributions for identity signals (Figure 2.6). In addition, most of these variable traits in Royal Tern chicks vary independently of one another, thereby maximizing the number of color combinations and overall individuality of each nestling's appearance (Buckley and Buckley 1970).

Egg coloration is also often remarkably variable, and such variability may function in identity signaling, an idea that stands in contrast with the recently developed hypothesis positing a quality signaling role for egg coloration (Moreno and Osorno 2003). For example, in Common Murres (*Uria aalge*), the background color of eggs varies from white to deep blue, with a foreground of variably colored spots, splotches, and streaks (Plate 8). Murres nest in dense colonies, and eggs can get jostled away from nesting positions. Tschantz (1959) demonstrated that murre parents use egg coloration to discriminate their own eggs from those of neighbors. Egg coloration in murres appears to demonstrate the expected properties for identity signals. In particular, color saturation is

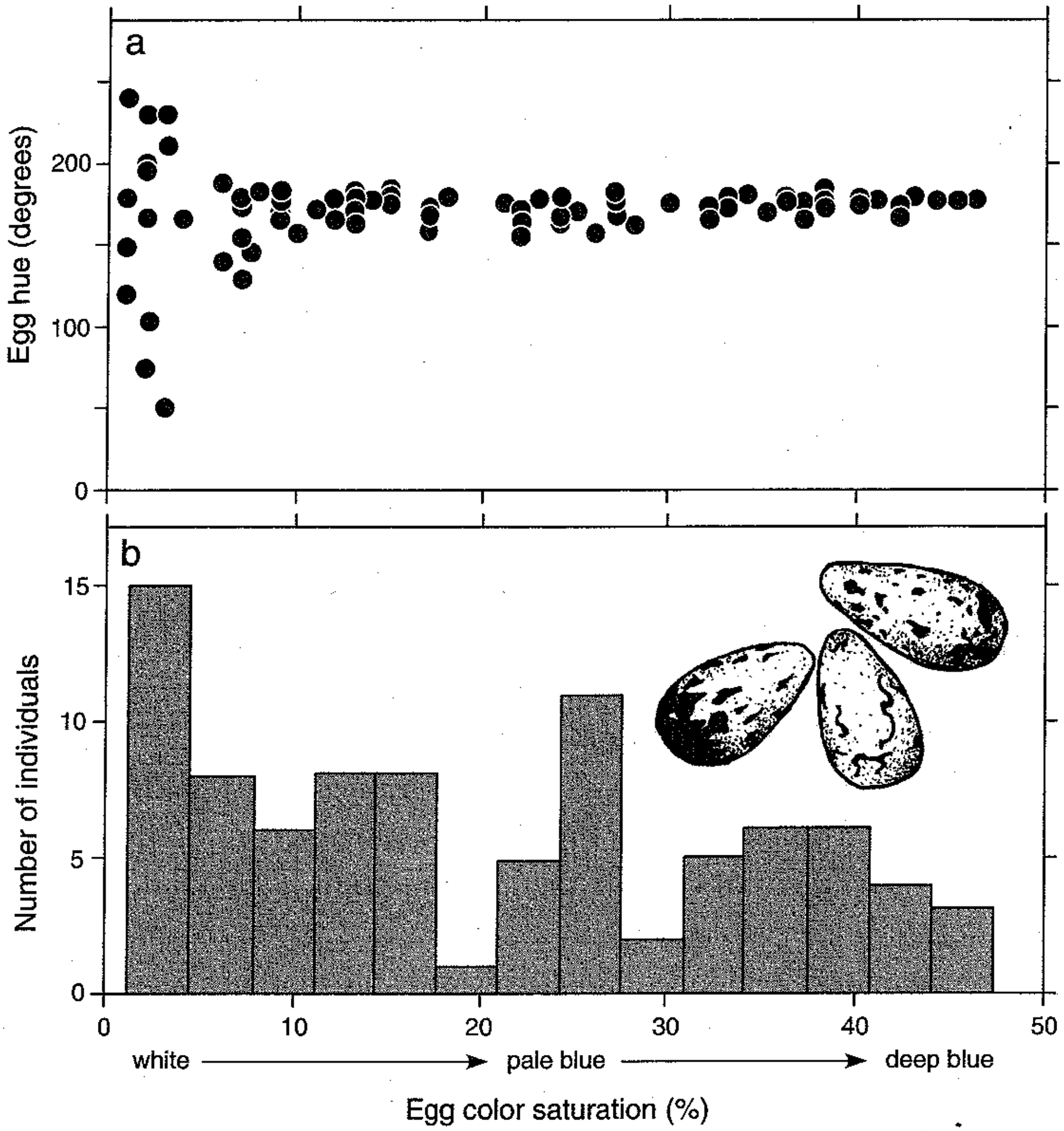

Figure 2.7. Variability in the background (not spot or blotch) coloration of Common Murre eggs ($n$ = 85) at a breeding colony on Triangle Island, British Columbia (J. Dale, unpubl. data, with color scored as in McGraw et al. 2003). (a) As egg color saturation approaches zero, hue becomes less meaningful as a measure of perceivable variability and hence becomes more variable (see Box 2.2). (b) Frequency distribution of background color saturation demonstrates an overall flat, possibly polymodal, pattern, as expected for identity signals.

highly variable among eggs, and the frequency distribution of saturation is remarkably uniform across the range of expression (Figure 2.7).

## Presence

One of the most important bits of information that individuals can signal about themselves is their presence—their immediate occupation of a particular location. Bright coloration makes an individual more conspicuous. Revealing presence can be crucial. For example, breeding males need to be easily located by females prior to courtship. In contrast, dull or cryptic coloration makes individuals less conspicuous. Concealing presence can also be crucial, for example, to avoid detection by predators or prey. Conspicuous and cryptic coloration are thus extremes of a range of color detectability (Endler 1988).

### Honest Signals of Presence

Reliable signals of presence should contrast strongly with the ambient light environment (Endler 1990) and be tailored to the sensory biases of the intended receivers (Rowe and Skelhorn 2004). Sensory exploitation or sensory bias (Endler and Basolo 1998) hypotheses to explain male breeding displays argue that displays increase mating success through an increased stimulation of the female sensory system. Certain colors or patterns could thus function to make a male's phenotype more obvious to potential mates.

If a color pattern is selected to reveal only presence, what are the expected properties of such a signal? Under the assumption that strong stabilizing selection drives such signals to fixation, then presence signals should demonstrate relatively low variability, display unimodal distributions, be cheap to produce (or, more specifically, not be differentially costly), develop in a way that is not environmentally dependent, and express a high degree of genetic determination with low degrees of heritability (i.e., low degrees of genetic diversity). Signals of presence should contrast strongly with ambient background conditions and should be conspicuous to the particular receivers whose behavioral responses benefit the signaler.

Presence signaling can easily give rise to sexual dichromatism. In bustards (Otididae) and plovers (Charadriidae), males tend to have more black coloration in species for which males include acrobatic aerial components to their breeding displays (Dale 1992; Bókony et al. 2003; Figure 2.8). Dark plumage contrasts strongly with the sky (Walsberg 1982) and could benefit males by making them more visible during display and therefore more easily located by females.

Presence signaling can also have benefits outside mate attraction. For example, Greater Honeyguides (*Indicator indicator*) have conspicuous white outer tail feathers that they flash repeatedly during displays designed to encourage humans to follow them to honeybee colonies (Isack and Reyer 1989). Killdeers (*Charadrius vociferus;* Plate 6, Volume 1) have orange rumps that they

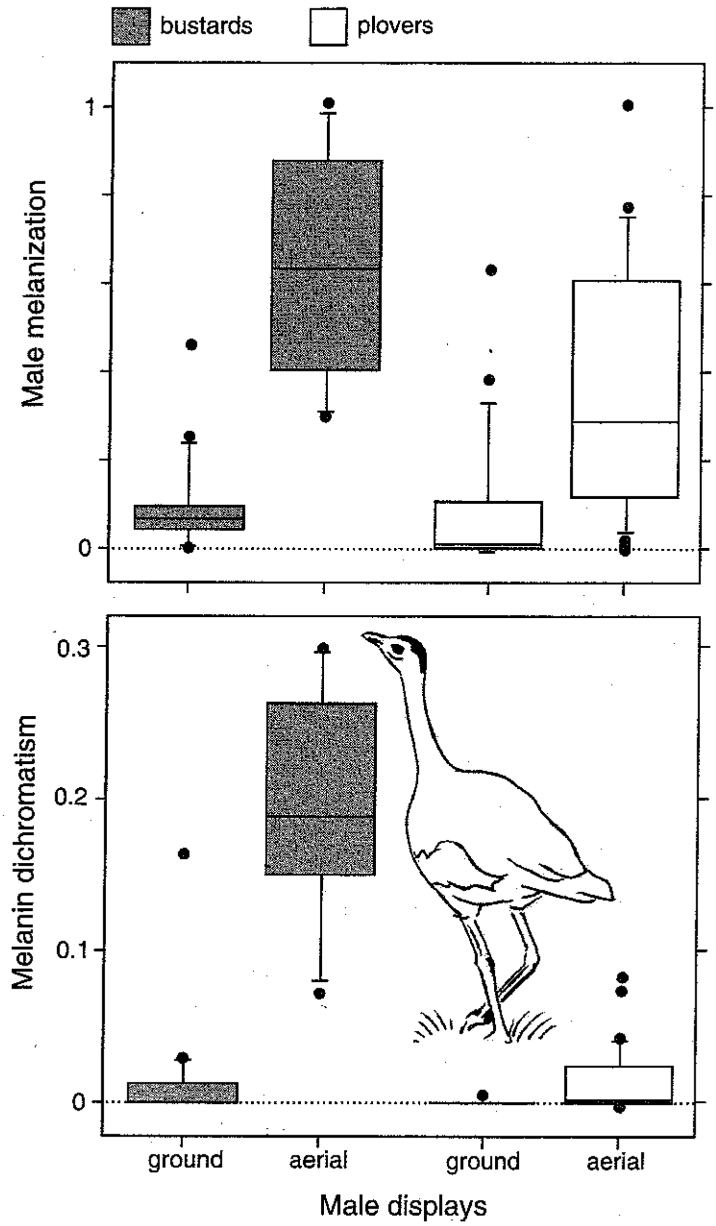

Figure 2.8. Male melanization (percentage of frontal body region that is black) and melanin dichromatism [log (male melanization + 1) – log (female melanization + 1)] in bustards (Dale 1992; J. Dale and J. Joy, unpubl. ms) and plovers (Bókony et al. 2003) as a function of male display type. Box plots show medians; 10th, 25th, 75th, and 90th percentiles; and all outlying data points. Data plotted are species values (bustards, $n$ = 23; plovers, $n$ = 45). In both groups, phylogenetically controlled analyses demonstrate that aerial displayers tend to be significantly more black than ground displayers.

flash to predators during distraction displays that lure predators away from their ground nests (Jackson and Jackson 2000). The bright yellow feet of Snowy Egrets (*Egretta thula*) are proposed to startle aquatic prey in murky pools (Parsons and Master 2000).

Aposematic coloration patterns are also conspicuous signals directed toward potential predators (receivers) and coupled to information about aspects of prey (signaler) unprofitability, such as toxicity (Dumbacher et al. 1992), unpalatability (Cott and Benson 1970), or alertness (also see Lyon and Montgomerie 1985; Endler 1988; Andersson 1994). Aposematic colors should be distinctive to receivers, so that they are easily remembered, and should contrast strongly with the background (Endler 1988).

## Cryptic Coloration

Cryptic color patterns are "dishonest signals of presence." Signalers benefit from concealing their presence by minimizing their contrast with the surrounding habitat (Endler 1988; Chapter 1). The signal is deceitful because receivers suffer fitness costs as a result of the deception. Thus receivers will be under strong selection to discriminate these deceitful signals, and arms races are expected between increasingly cryptic signalers and increasingly perceptive receivers.

Cryptic signals are expected to express similar properties as honest (i.e., conspicuous) signals of presence, except they should be difficult to detect. Because cryptic coloration often involves contrasting bands, patterns, and spotting typically involving a variety of earth-tone colors, such coloration should generally be more complex and variable than coloration designed to make signalers more obvious. Overall complexity (and variability) of cryptic coloration is thus expected to co-vary with the degree of heterogeneity of the usual background (Endler 1988).

When a single species occupies different habitats with different backgrounds, cryptic coloration should vary across those habitats, such that contrast is minimized optimally across the different landscapes (Endler 1988). Thus increased intraspecific variability in cryptic coloration can occur when (1) there are seasonal changes in the habitat's ambient conditions, (2) there are different ambient conditions at breeding and nonbreeding locations, or (3) the occupied habitat is naturally variable. The first two conditions increase interclass variability (i.e., seasonal variability) whereas the latter condition increases intraclass variability.

Because background conditions can undergo dramatic seasonal changes, cryptic coloration is expected to track those changes. For example, Rock Ptarmigan (*Lagopus muta*) maintain residency throughout the year in the high arctic. During winter, when their world is a snowscape, ptarmigan are a uniform brilliant white. During summer, when the habitat is earth-tone, ptarmigan molt to a mottled, cryptic brown (Plate 19, Volume 1). Interestingly, males maintain their white winter plumage during early summer, despite the dangers of increased predation, possibly because white plumage may increase a male's ability to attract females (Montgomerie et al. 2001). After males acquire mates, however, they smear dirt into their plumage to make it less conspicuous (Montgomerie et al. 2001; Chapter 9, Volume 1). Thus males actively manipulate their plumage from an honest to dishonest signal of presence.

Birds often migrate to breeding and nonbreeding locations that vary dramatically in their backgrounds, and cryptic signaling is expected to co-vary with those changes. For example, in summer, Marbled Murrelets (*Brachyramphus marmoratus*) have a cryptic brown plumage that conceals their presence on the tree limbs on which they nest. In contrast, wintering murrelets live an entirely pelagic lifestyle, and in this environment, they display typical light below and dark above countershading commonly observed in ocean-dwelling birds (Nelson 1997). Such patterns are generally argued to conceal the birds to prey below and from predators above (Ruxton et al. 2004; Chapter 1).

When a species occupies habitats with natural background variability, then cryptic coloration is expected to be polymorphic (i.e., the occurrence in one population of two or more sharply distinct and genetically determined forms; Huxley 1955). In the first comprehensive comparative survey of polymorphism of birds, Galeotti et al. (2003) found that polymorphic species (estimated to be 3.5% of all species) tended to be active during both day and night and tended to occupy multiple and/or semi-open habitats. They concluded that these patterns suggest that avian plumage polymorphism probably evolved under selective pressures related to bird detectability, as affected by variable backgrounds (although it is important to keep in mind that other signaling functions, such as conveying strategy or individual identity, can also give rise to polymorphisms). In Arctic Terns (*Sterna paradisaea*), for example, chicks are either gray or brown (Lemmetyinen et al. 1974), and this polymorphism appears to be maintained by the mosaic-like nature of their nesting environment. In areas dominated by gray rocks and sparse vegetation, gray chicks are more frequent, whereas in areas with more brownish soil and denser vegetation, brown chicks predominate.

## Apostatic Selection

The avoidance image hypothesis (Paulson 1973; Rohwer and Paulson 1987) is a form of dishonest presence signaling that occurs independently of ambient backgrounds and is specifically based on receiver psychology. The hypothesis posits that receivers (prey or predators) form search images based on the most common phenotypes of the signalers (predators or prey, respectively). Rare signaler phenotypes can therefore be at a selective advantage, provided they are less likely to be recognized.

The apostatic hypothesis has been developed with particular attention toward explaining high degrees of color variability in raptors (Paulson 1973; Rohwer and Paulson 1987). Alternatively, however, individual identity signaling could explain raptor plumage diversity (see the section on identity above). It is interesting to note that the two hypotheses are reversed versions of one another. In identity signaling, rare morphs benefit due to *increased* recognizability to conspecifics. In avoidance image signaling, rare morphs benefit due to *decreased* recognizability as a threat to prey. Although the assumptions regarding receiver psychology are completely different between the two hypotheses, the outcome of the two processes are the same and are expected to result in highly similar signal properties. That is, apostatic selection is negatively frequency-dependent (Rohwer and Paulson 1987; Endler 1988) and is thus expected to result in high degrees of genetically determined color variability that demonstrate complex frequency distributions (e.g., see Dale et al. 2001). Apostatic selection is not expected to result in increased interclass variability, such as sexual dichromatism (Fowlie and Kruger 2003).

Although apostatic selection has been demonstrated to be a potentially important process with Blue Jays (*Cyanocitta cristata*) hunting virtual insect prey (Bond and Kamil 2002), the hypothesis has generally been argued to be an unlikely selective force driving increased variability in bird coloration (Preston 1980; Fowlie and Kruger 2003; Galeotti et al. 2003; but see Roulin and Wink 2004). One of the key predictions of apostatic selection is that polymorphic raptors should prey upon more intelligent prey, such as birds and mammals, because these prey are argued to be more likely to form search images of predators that they have previously encountered (Paulson 1973; Roulin and Wink 2004). However, intelligent prey should arguably be less likely fooled by alternative plumage patterns in raptors when other cues are readily available for identifying unfamiliar predators. For example, prey should be strongly selected to base their recognition template of predators on more reliable cues, such as a silhouette (Preston 1980; Galeotti et al. 2003). In my view, due to strong territorial behavior in birds of prey, individual identity signaling represents a promising and hitherto unexplored hypothesis to explain their remarkable plumage diversity.

## Discussion

I have restricted the hypotheses covered in this synthesis to signaling functions related to color variability. However, alternative nonsignaling functions are also critically important for understanding bird colors. For example, thermoregulation (Burtt 1981), mechanical benefits of pigmentation (Butler and Johnson 2004), and protection from bacterial degradation (Goldstein et al. 2004), solar UV radiation (Ward et al. 2002), and glare (Burtt 1984) are all important hypotheses (see Chapter 1). Because adaptive nonsignaling coloration will generally be under strong stabilizing natural selection, it is expected to be genetically fixed and express low degrees of phenotypic variability. Interclass variability (see Box 2.1) in coloration with nonsignaling functions is also expected to be reduced, although some hypotheses, such as thermoregulation, do predict geographical clines of variation (Galeotti et al. 2003).

Variability in coloration can also have no function, resulting simply from mutations that are not influenced by selection (Kimura 1962, 1983). Indeed, one of the most obviously variably colored birds, the Snow Goose (*Chen caerulescens*), appears to have plumage variability not associated with any function (Cooke et al. 1995). Despite long-term observations and massive datasets, Snow Goose researchers have failed to find any fitness correlates with this highly conspicuous variability. Plumage variation is instead argued to be the result of different morphs evolving in allopatry, followed by a recent secondary introgression (Cooke et al. 1995; Lank 2002). The neutral hypothesis can clearly be highly relevant for understanding large-scale plumage variability, although Snow Geese represent the only well-developed case study so far.

To refute the null hypothesis that plumage variability is not related to a communication function, the demonstration of fitness benefits associated with signaling is required (e.g., see Box 2.3). Additional evidence that can support the hypothesis that color displays have evolved as signals include (1) a trait has apparent signal design (e.g., if it is highly conspicuous, sexually dimorphic, or behaviorally enhanced during social interactions), (2) variability in coloration influences behavior in receivers (e.g., Whitfield 1986), or (3) an interspecific association occurs between color variability and the socioecological variables that are expected to relate to signaling (e.g., Galeotti et al. 2003).

### Nonmutually Exclusive Hypotheses

The different dimensions of information revealed through plumage coloration (see Table 2.2) represent alternative explanations for variability. These hypotheses are not mutually exclusive, because any variability in coloration could potentially reveal multiple aspects of information about an individual to multiple receivers. Color patterns could therefore be compromises of various signaling functions (Endler 1988). For example, a sexually dimorphic color trait could have been shaped by selection through cumulative benefits associated with revealing quality, attractiveness, strategy, and presence.

Alternatively, different color traits within an individual could reveal completely different information. Consider breeding male Red-billed Queleas, which have two separate color-based signaling systems: (1) complex and independently assorting variability in various plumage features reveals individual identity, whereas (2) unimodally distributed coloration in bare parts (bill, leg, and eye-ring) reveals quality (Shawcross and Slater 1983; Dale 2001; Figure 2.9). In the Ruff, males reveal at least three separate types of information about themselves with different color-based traits: (1) bimodally distributed plumage patterns reveal male strategy; (2) additional complex plumage variability within each strategy type reveals individual identity; and (3) facial wattle area (number of caruncles), which is age-dependent, presumably reflects quality (Dale et al. 2001; Lank and Dale 2001).

### Multiple Ornaments

Currently there is widespread interest in why birds have multiple ornaments (Møller and Pomiankowski 1993; Johnstone 1996; Candolin 2003). The basic theoretical framework is centered around three hypotheses developed in a groundbreaking paper by Møller and Pomiankowski (1993): (1) multiple messages, (2) redundant messages, and (3) unreliable signals. These hypotheses essentially reduce the problem of multiple ornaments to only one kind of information: quality. The multiple messages hypothesis argues that the information content of the two traits reflect different aspects of quality. The redundant messages hypothesis argues that the information content of each trait

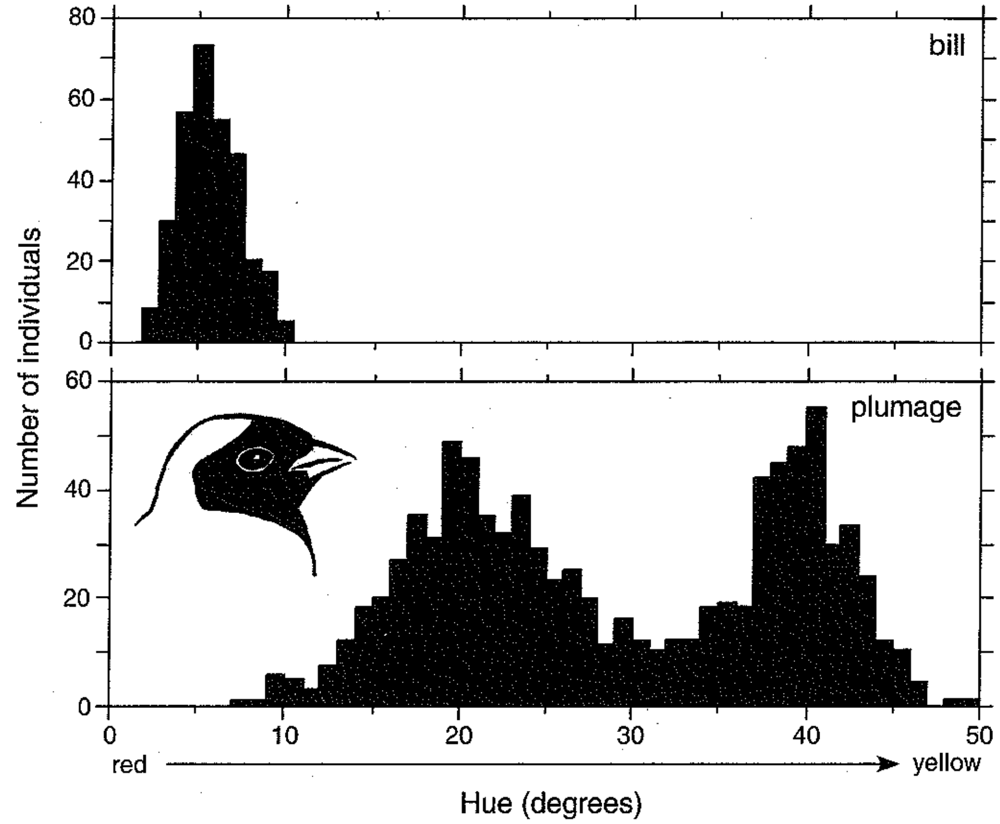

Figure. 2.9. Dual signaling system of male Red-billed Queleas. Unimodally distributed bill hue ($n = 324$) signals quality, whereas bimodally distributed plumage hue ($n = 897$) signals individual identity. Color scores measured using methodology described in Dale (2000). Adapted from data in Dale (2000, 2001).

reveals similar aspects of quality. For receivers to be selected to favor redundant messages, the increased reliability of information provided by traits in combination must be high enough to offset the additional costs to receivers associated with processing multiple signals (Johnstone 1996). Finally, the unreliable signals hypothesis argues that ornaments do not reveal quality and are the product of, for example, separate instances of Fisherian runaway selection occurring independently on separate traits.

To understand the origin of multiple ornaments, we need to understand all the potential information types revealed by traits (see Table 2.1), not just quality (Candolin 2003). Furthermore, we require an understanding of how different information types interact, overlap, and trade off with one another (Johnstone 1996; Candolin 2003) and who the intended receivers are for different signals (see Andersson et al. 2002). Resolving the different functions of multiple ornaments in birds is an exciting avenue for future research.

By evaluating the properties of different traits within a species (see Table 2.2), we can gain insights into the diverse messages revealed by them (e.g., see Figure 2.9). Multiple messages are likely the norm in birds, and this will especially be true when all potential types of information revealed by color-based signals are considered, as well as additional "ornamental" phenotypes, such as song, smell, and behavioral display.

## Conclusions

At the beginning of this chapter, I asked why American Crows are so uniform and Ruffs are so diverse. With Ruffs, plumage likely signals multiple messages, including strategy, individual identity, and quality. With crows, I can only hazard some speculative guesses. Assuming that there is a signaling function to crow blackness, then crow plumage has the basic properties expected for signals that function as (1) amplifiers, (2) species identifiers, and (3) indicators of presence. First, crows could use UV coloration to signal quality. Indeed on close inspection, adults have a violet-blue gloss on the body and a greenish-blue gloss on the wings. Therefore crows might not be so uniform, after all. However, putatively variable UV-signaling in crows still begs the question of the reason for the uniform blackness that underlies it. One possibility is that crow blackness functions as an amplifier to the UV signals. Second, low variability in crow blackness could function as a signal of species identity. However, it is unlikely that blackness signals species identity with respect to mate choice, because other species of sympatric and closely related corvids (e.g., Fish Crows [*Corvus ossifragus*]) are also completely black. Finally, crow blackness could function as a signal of presence to facilitate flocking or alternatively, to advertise territorial occupancy. Indeed, crows are known to form massive flocks during winter and at roosts (Verbeek and Caffrey 2002). Black coloration contrasts strongly against most natural backgrounds, including the sky (Walsberg 1982), so both perching and flying crows are highly visible, even at great distances. That crows are such noisy creatures does indeed suggest that selection has favored conspicuousness in this species.

The problem of crow blackness illustrates a final point that is often overlooked. High variability in plumage coloration may be easier to explain than low variability. A challenge for future studies of plumage coloration is to explain why so many species are (apparently) so uniform. Moreover, what exactly is the distribution of color variability across different species? The question of why there is such high "variability in color variability" remains open for future studies of avian coloration. Indeed, the nature of intraspecific variability in all signaling media in all organisms is a rather poorly understood aspect of communication.

## Summary

There are considerable differences among bird species in the degree of color variation within populations. In some species, there appears to be little difference among individuals, whereas in other species, each individual seems to be unique. Why is there so much interspecific variation in within-species variability? Here I have argued that general patterns of intraspecific variation can be understood from a communication-based theoretical framework in which signalers reveal information about themselves to receivers. Birds use color to reveal seven broad kinds of information—quality, Fisherian attractiveness, behavioral strategy, genetic compatibility, kinship, individual identity, and presence.

Quality signals reveal information about relative phenotypic and genetic constitution and are expected to express relatively high degrees of unimodally distributed, environmentally determined (condition-dependent) variability. In addition, quality signals can be associated with "amplifiers," traits that increase the receiver's perception of ornament elaboration. In contrast to quality signals, amplifiers are expected to be fixed and express low variability.

Fisherian runaway selection results in traits that define attractiveness independent of quality. Fisherian traits are expected to be intense colors that demonstrate relatively low intrapopulation variability and high geographic variability (provided that different populations arrive at different equilibrium states).

Strategy signals are expected when individuals form strategy-dependent cooperative alliances and include signals of gender, some forms of delayed-plumage maturation, and signals of mating strategy. Strategy signals are expected to be bimodally distributed (one mode for each strategy) and can be genetically or environmentally determined, depending on the specific strategies revealed.

Traits that reflect genetic compatibility for mate choice include species isolation signals and signals of genetic similarity. Species isolation processes (reinforcement and species recognition) provide the most promising scenarios in which to find color-based compatibility signals. Such signals are expected to be genetically fixed traits that express low variability within genetically distinct populations and high variability between them.

Kinship signals facilitate discrimination of unfamiliar kin and can be stable for color-based signals, provided that signalers frequently encounter and interact with unfamiliar relatives. Such signals are expected to be based on multiple, variable, and independently assorting traits based on polymorphic loci scattered throughout the genome.

Individual identity signals are "name tags" that increase overall recognizability. Signaling individual identity by color display might be widespread in birds and appears to be associated with the highest degrees of observed variability in coloration. Identity signals often display complex, multimodal distributions presumably arising from negative frequency-dependent selection acting on signal phenotypes. They are expected to express similar properties as kinship signals; however, identity signals are only used to discriminate familiar individuals (i.e., the signal must be learned by receivers).

Finally, signals of presence either reveal (honest signals) or conceal (dishonest signals) an individual to receivers. Such signals should contrast (or blend) with the ambient environmental conditions and generally be fixed traits that express low degrees of unimodal variability. However, variable background conditions can easily give rise to increased phenotypic variability, particularly with cryptic coloration.

These seven signal types represent non-mutually exclusive alternative communication functions for bird coloration and provide a rich arena for the provision of multiple messages by signalers. Furthermore, the framework developed here is expected to be general and should provide insight into signaling in all communication channels in all taxa.

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