Visual Signals for Individual Identification: The Silent “Song” of Ruffs

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

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

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

We examine to what extent the most prominent plumage characteristics of breeding male Ruffs vary independently. Previous analyses have produced conflicting results (Table 1; van Rhijn 1991). We revisit that question using automated and quantitative measurements of plumage characteristics, and by
considering whether two behavioral types of male ruffs, which differ in predominant plumage colors, should be analyzed separately.

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

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

Lekking males advertise their presence at long distances by flashing their wings or hovering over courts when they detect flying Ruffs (Hogan-Warburg 1966, Widemo and Owens 1995). All other intra- and intersexual display occurs at close quarters on the ground (Hogan-Warburg 1966, van Rhijn 1997, Widemo 1998). The behavioral difference between territorial and satellite morphs is determined by alternative alleles of a balanced genetic polymorphism (Lank et al. 1995, 1999; Widemo 1998), and plumage differences also appear to have a genetic basis (Lank and Smith unpubl. data).

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

We quantified four characteristics of Ruff breeding coloration. (1) **Ruff shade**: to simplify the analysis of ruff coloration, we used Photoshop's "Histogram" function to reduce color to a grayscale value ranging from black (= 0) to white (= 255). Under that scale, brown is measured as dark grey, whereas shades of brown or rusty colored ruffs but white head tufts are lighter grey. We scored only the predominant shade in the ruff when more than one shade was present. We divided scores by 2.55 to produce a scale ranging from 0 (=black) to 100 (=white). (2) **Head tuft shade**: if several shades were present, we scored the predominant shade at the end of the head tufts. (3) **Wattle hue**: scoring the predominant shade at the end of the head tufts. (4) **Wattle hue**: to simplify the analysis of ruff coloration, we used Photoshop's "Histogram" function to reduce color to a grayscale value ranging from black (= 0) to white (= 255). Under that scale, brown is measured as dark grey, whereas shades of brown or rusty colored ruffs but white head tufts are lighter grey. We scored only the predominant shade in the ruff when more than one shade was present. We divided scores by 2.55 to produce a scale ranging from 0 (=black) to 100 (=white).

**Results.**—Both plumage brightness characters had complex multimodal distributions, with high frequencies of predominantly black tracts and a spread across other shades (Fig. 1A, B). The modality of wattle colors was difficult to resolve with that sample (Fig. 1C), but may be uni-, bi-, or even trimodal, with peaks at red, orange, and yellow (c.f. van Rhijn 1991). Patterns were distributed evenly (Fig. 1D), but this could change with the system of categorization. The independent variation of Ruff plumage characters is consistent with the hypothesis that variation evolved specifically to facilitate individual recognition (Beecher 1982, Dale et al. 2001). A popular alternative functional explanation for plumage variation in other species is that it indicates aspects of a male's condition, or quality (Rohwer 1975, Andersson 1994, Hill and Montgomerie 1994). Signals evolved to identify individuals should not be condition-dependent, and not correlate with fitness (Dale et al. 2001). Evidence against condition-dependence is that despite uniform rearing conditions, characters are not significant (Table 2).
captive-reared populations display the full range of color variation observed in the wild (D. Lank and C. M. Smith unpubl. data). Male Ruffs do have age and condition-dependent characters that do correlate with mating success, including the length and density of display plumes, extent of facial wattles, and leg and bill color, as well as behavioral displays and social interactions (Shepard 1975, Hill 1991, Widemo 1997). In sharp contrast, however, all authors conclude that plumage coloration is not correlated with mating success (Selous 1906–1907, Hogan-Warburg 1966, Shepard 1975, Hill 1991, van Rhijn 1991, D. Lank and C. M. Smith unpubl. data).

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

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

![FIG. 1. Frequency distributions of four characters measured in the breeding coloration of male Ruffs (n = 82). Separate distributions are shown for residents (black bars) and satellites (grey bars). (A) ruff shade, (B) tuft shade, (C) wattle hue, (D) ruff pattern. See methods for scaling and categorization.](image-url)
TABLE 2. Correlations between plumage and wattle characters in male Ruffs. Results of analysis are given for the entire sample of males (upper right matrix) and for the sample with satellites excluded (lower left matrix). Spearman rank correlations were used to evaluate relationship between continuous quantitative characters, and Kruskal-Wallis tests were used to evaluate relationship between pattern (a categorical character) and the quantitative traits. Boldface indicates $P < 0.05$.

<table>
<thead>
<tr>
<th></th>
<th>Ruff</th>
<th>Head Tuft</th>
<th>Wattle</th>
<th>Pattern</th>
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<tbody>
<tr>
<td></td>
<td>(Satellites included)</td>
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<tr>
<td>Ruff</td>
<td>$Rho = 0.14$</td>
<td>$Rho = 0.16$</td>
<td>$H = 5.5$</td>
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<td></td>
<td>$n = 77$</td>
<td>$n = 62$</td>
<td>$n = 81$</td>
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<td></td>
<td>$P = 0.21$</td>
<td>$P = 0.22$</td>
<td>$P = 0.14$</td>
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<td>Head tuft</td>
<td>$Rho = -0.16$</td>
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<td></td>
<td>$n = 62$</td>
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<td></td>
<td>$P = 0.19$</td>
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<td>$P = 0.33$</td>
<td>$P = 0.005$</td>
</tr>
<tr>
<td>Wattle</td>
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<td>$H = 5.2$</td>
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<td></td>
<td>$n = 51$</td>
<td>$n = 51$</td>
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<td></td>
<td>$P = 0.07$</td>
<td>$P = 0.27$</td>
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<tr>
<td>Pattern</td>
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<td>$H = 4.8$</td>
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<td></td>
<td>$n = 69$</td>
<td>$n = 66$</td>
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<td></td>
<td>$P = 0.59$</td>
<td>$P = 0.007$</td>
<td>$P = 0.19$</td>
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<td>(Satellites excluded)</td>
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Silence on the lek is not entirely restricted to Ruffs. Several other species with ground-displaying males use little vocalization once females are on mating courts. Buff-breasted Sandpipers (Tryngites subruficollis), a close relative of the Ruff, in which males defend moderately sized, clumped-lek territories, have nearly silent close-range courtship (Lanctot and Laredo 1994). Despite their notorious long-distance calls, courting peafowl (Pavo cristatus) do not vocalize in that situation.

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

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**Frequency of Egg and Nestling Destruction by Female Brown-headed Cowbirds at Grassland Nests**

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ABSTRACT.—Researchers have suggested that Brown-headed Cowbirds (*Molothrus ater*) destroy nest contents of potential hosts to induce renesting and thus enhance future opportunities for parasitism. Although cowbird destruction of passerine nests has been witnessed and surmised, few data are available on frequency of those events. We used miniature video-cameras at nests of grassland passerines and documented partial or complete destruction of eggs or nestlings by cowbirds at 7 of 132 nests monitored with cameras. At least three of the seven cases appeared to be attempts to totally destroy the nest contents; those cowbirds did not appear to be motivated by food or an intent to parasitize the nest. Three cases probably were associated with parasitism, but two involved egg removal late in incubation and the third was unusually destructive. Cowbirds were responsible for 24% of egg losses and 5% of nestling losses caused by predators. The importance of cowbirds as an agent of egg and nestling loss undoubtedly varies among sites and years, but it should not be overlooked.

Brood parasites lay eggs in nests of other birds and potentially depress host productivity in several ways. The most frequently reported effects of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) are removal of host eggs in conjunction with laying their own eggs and competition of cowbird nestlings with host nestlings for food (Robinson et al. 1995). In addition, adult cowbirds may function as predators (Arcese et al. 1996, De Groot et al. 1999); female cowbirds have been observed removing eggs from unparasitized nests of potential hosts without subsequent parasitism (Blincoe 1935, Potter 1985), and have been seen killing nestlings of host species (Du Bois 1956, Tate 1967, Beane and Alford 1990, Scott and McKinney 1994, Sheppard 1996, Elliott 1999). Arcese et al. (1992) found that nest success for an insular population of Song Sparrows (*Melospiza melodia*) was lower when Brown-headed Cowbirds were present, but that predation rates were higher on unparasitized than on parasitized nests. Early research on brood parasitism asserted that Old World cuckoos destroy host nestlings to induce renesting, thus increasing opportunities for brood parasitism (Jourdain 1925). Arcese et al. (1996) hypothesized that cowbirds destroy nests of potential hosts for the same reason.

Although cowbird destruction of passerine nests has been witnessed and surmised, few data are available on frequency of those events. Thompson et al. (1999) reported a cowbird attack on nestlings at one of 52 nests monitored with video cameras, although no nestlings died. We previously reported videotaped evidence of cowbirds destroying contents of two grassland passerine nests (Pietz and Granfors 2000). Here we provide additional evidence of cowbirds destroying eggs and nestlings, quantify parasitism frequency and the frequency of egg and nest-