Colour schemes for birds: structural coloration and signals of quality in feathers

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Plumage coloration may signal individual quality through carotenoid and melanin colour patterns; novel mechanisms by which structural coloration in feathers could signal individual quality are proposed here. Uniformity of structural colour is suggested to signal developmental stability during feather growth, the colour constituting an amplifier. For structural coloration produced by coloured portions of barbules which are susceptible to loss by abrasion, the intensity of colour is suggested to signal feather quality and abrasion-resistance, the structural colour constituting an amplifying handicap. In both cases, large areas of structural coloured plumage may be more revealing of quality than small areas. Predictions as to the extent, position and combinations of these structural colours relative to carotenoid and melanin coloration were derived from these mechanisms and supported by comparative tests. Structural coloration may thus be a component in multiple messages of individual quality in plumage coloration.

1. Introduction

1.1. Colour signals in plumage

The evolution of colourful plumage in birds has long been associated with its signal function (Darwin 1871), but as yet we have little understanding of the reasons for particular colour schemes. Overall conspicuousness has been considered to be of major signalling importance (e.g., Baker & Parker 1979, Hamilton & Zuk 1982, Endler 1990), in which case the evolution of differential coloration between species is guided by differential environmental influences on conspicuousness (Endler 1992), and driven by Fisherian sexual selection ensuing from arbitrary colour preferences or sensory bias (Ryan & Keddy-Hector 1992). If,

however, particular colours signal differential aspects of individual quality, the evolution of coloration will also involve handicap (Zahavi 1975) or amplifier (Hasson 1989) mechanisms of signal selection. The signals inherent in colour *per se* or in the details of colour patterning have been relatively neglected, but recent studies have suggested that particular colours and colour combinations have the potential to indicate individual quality.

The potential of carotenoid-based colours (red and yellow) to indicate individual quality during mate choice in birds is now well established (Hill 1990, 1991, Johnson *et al.* 1993, Piersma & Jukema 1993, Hill & Montgomerie 1994, Sundberg & Larsson 1994, Dufva & Allander 1995, Sundberg 1995ab, Sundberg & Dixon 1996, Linville *et al.* 1998). Either the colour intensity or the extent of

the coloured area have been found in these studies to correlate with some individual quality, the diet, condition, general health, immunocompetence and parasite resistance, viability, or parental care. Red and yellow carotenoid colours, when incorporated into avian colour schemes, thus may be indicating some important aspect of their bearer's intrinsic qualities.

As absence of melanin weakens keratin and increases feather abrasion (Burtt 1986, Bonser 1995), pale regions of feathers, such as white tips on the tail, may indicate feather quality by acting as amplifying handicaps (Fitzpatrick 1998a). Amplifiers are signals increasing the perceptibility of quality (Hasson 1989, 1991), in this case making abrasion and/or breakage more visible. However, as the white area also increases the likelihood of abrasion and damage in individuals with poor quality feathers, a quality-specific cost is incurred due to the signal — it is a handicap (Zahavi 1975, Grafen 1990). A comparative survey of tail patterns supported this suggested signal function (Fitzpatrick 1998a), and one field study so far (Wiehn 1997) has shown variations in melanin-based markings correlating with individual quality in a way consistent with their being such amplifying handicaps.

Barred feather markings have been proposed as amplifiers of growth bar cues of feather growth regularity (Hasson 1991). Regularity or irregularity of melanin-deposition bars within a feather, and the degree of registration of barring patterns across adjacent feathers, may thus constitute an indicator of developmental stability during feather growth. Unfortunately, this idea has apparently not yet been explored further.

The remaining commonly found colours in avian plumage are structurally-produced coloration; two major types will be discussed here. The first type, involving barbs (filaments branching from the feather shaft) and/or all barbules (filaments branching from barbs), frequently produces blue and bright green colours and is referred to here as plain structural coloration. The second type, referred to here as glossy structural coloration, involves only specialized portions of some barbules and produces glossy, iridescent plumage, often with an underlying black (melanin) coloration. Gray (1996) dismissed the possibility of structural coloration being a quality-indicating

signal because of an apparent lack of associated handicapping costs, but recent studies suggest just such a signal function for structural coloration in several species (Andersson & Amundsen 1997, Andersson 1998, Andersson *et al*. 1998, Hunt *et al*. 1998). An 'honesty-maintaining' mechanism in structural coloration is therefore necessary (Andersson 1998). Amplifiers are quality-indicating signals which do not necessarily entail handicapping costs (Hasson 1989), the quality-correlation of the signal being maintained by higher social costs to poor quality individuals over-expressing the amplifying signal. Even without being a handicap, structural coloration could therefore act as an amplifier. Detailed consideration of these types of structural coloration suggests two potential mechanisms by which they could constitute quality-indicating signals, as described in the next section.

1.2. Quality-indicating potential of structural coloration

Structural coloration of both types depends on the microstructure of the coloured part of the feather. Structural coloration can be based on either wavelength-differential reflections or interference patterns of light arising from keratin/melanin, keratin/air or melanin/air interfaces inside the feather (Dyck 1976). For wavelength-differential reflections, the reflected wavelengths producing the colour mainly depend on the depth, nanometre-scale dimensions and alignment of the keratin rods, air spaces and melanin granules in the feather barbs (Dyck 1976). Minute variations in these dimensions occurring during feather growth would alter the wavelength reflected and hence the resulting colour. To produce a plumage area of uniform colour thus requires a high degree of precision during feather development; the larger the area of plumage of uniform colour, the longer the period of precise developmental stability necessary. Similarly, colour production by interference phenomena would also be crucially altered by nanometre-scale variations in the dimensions of the interfaces involved. Structural coloration thus has the potential to constitute an indicator of developmental stability and precision during feather growth, making developmental stability or in-

stability perceptible through the colour and its variation.

Where the structural coloration is produced only on special flattened and angled portions of the barbules (Lucas & Stettenheim 1972), i.e. glossy structural coloration, the coloured parts of the barbules are connected to the barb by a twisted stalk, vulnerable to damage and abrasion (Lucas & Stettenheim 1972, Ginn & Melville 1983). By increasing the likelihood of abrasion of a quality-indicating colour, glossy structural coloration might constitute an amplifying handicap mechanism indicating feather quality, with some similarity to that already proposed for pale markings (Fitzpatrick 1998a).

Based on these potential quality-indicating features of structural coloration, tentative predictions can be made concerning the extent and position of structural coloration in comparison with carotenoid signals and melanin-plus-markings colour patterns, and the combinations of these quality-indicating colour schemes most likely to occur:

1. Structural colours of both types, if revealing developmental stability, should generally occur in areas of uniform coloration, without variation or markings. As the extent of the area of coloration is part of the indication of quality, structural coloration should occur over large areas of plumage.

2. As glossy structural coloration may indicate both developmental stability and feather quality, the strength of signal selection might be increased and lead to a greater area of glossy than plain structural coloured plumage.

3. The extent of carotenoid-based colours may be limited by either the availability of an externally acquired pigment or by processes during pigment-synthesizing metabolism (Hill 1992, 1996). Structural coloration will not suffer these constraints and thus the size of the area of structural coloration is potentially greater. Structural coloration is therefore predicted to occur in larger areas of uniform, unmarked plumage than carotenoid-based colours.

4. Quality-indicating melanin-based coloration should frequently include feather markings and thus the area of uniform colour should be reduced in comparison with all the other coloration types.

5. The final predicted order for extent of the total area of uniform coloured plumage is thus: glossy structural colour > plain structural colour > carotenoid colours > melanin colours.

6. A further prediction concerning the position of the colour on the bird's body can be made. As the dorsal surfaces of birds' plumage are subject to greater abrasion from airborne particles (Burtt 1986), the most effective position for abrasion-revealing coloration is on the head, back, wings and tail. Glossy structural coloration and melanin-plus-markings should therefore occur most frequently on these dorsal surfaces.

7. If glossy structural coloration and melanin-plus-markings are both potential indicators of feather quality, they should constitute alternative quality-indicating colour schemes and thus infrequently occur together on the same bird.

8. Similarly, if structural colour and melanin-based barring patterns are both potential indicators of developmental stability, they too should constitute alternative quality-indicating colour schemes and thus not occur together on the same bird.

9. For maximal indications of different qualities by plumage, the coloration of a bird should include (i) carotenoid colour — a general health indicator, plus (ii) an indicator of developmental stability — either through structural coloration or melanin-based barring, and (iii) an indicator of feather quality — either glossy structural colour or melanin-plus-markings. Carotenoid colours should thus frequently co-occur with structural coloration and with melanin-based coloration, but structural colours should infrequently co-occur with melanin-based colour patterns.

This study makes a preliminary investigation of whether these proposed mechanisms form part of the signalling system inherent in birds' plumage by testing these predictions in a comparative survey of bird coloration.

2. Methods

Illustrations of males in breeding plumage in major handbooks and monographs (*see* Appendix 1) were used to select species from the phylogenetic levels of family, sub-
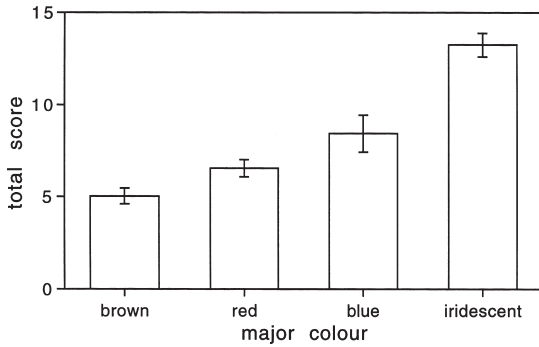
Fig. 1. Proportion of plumage coloration by major colours. Mean ± S.E. total colour score shown for each major colour.

family and tribe, according to the phylogeny of Sibley and Ahlquist (1990). The widely-occurring colours brown, red, blue and iridescent-black were selected as melanin, carotenoid, plain structural and glossy structural colours respectively. The carotenoid red was selected instead of yellow because a previous study (Hill 1996) has shown the area of red plumage to be an important variable. Plain structural blue was chosen in preference to green as there are several mechanisms of producing green plumage, some including pigments (Auber 1957). For each of the selected colours, candidate species were visually compared, without regard for colour uniformity or markings, and the species with the largest relative area of the colour in its plumage was selected for the lowest available phylogenetic level. A different species was selected for each colour. This colour was designated the major colour of the selected species. The resulting data set comprised 266 species from 90 families; 69 subfamilies and 35 tribes were represented from among these families. The maximum number of species from a single family (Fringillidae) was 21, all other families with the exception of Phasianidae, Corvidae and Muscicapidae having less than 10 representative species.

As an additional safeguard against the influence of phylogenetic bias on tests of predictions 1–5, and to provide *a priori* comparisons between colours, subsets of data forming independent pairwise comparisons were constructed for each possible pair of major colours. Two representative species at the same phylogenetic level differing in major colour constituted a matched pair.

For comparison of the areas of each major colour (predictions 1–6), in each selected species the extent of the colour was scored for males in breeding plumage for six body regions: head + neck, breast, belly, back, wings, and tail. The maximum extent of the major colour, uniform and uninterrupted by other markings, on each body region was assessed as a proportion of that body region, and scored as follows:

less than a quarter	score 0
one quarter to a half	score 1
half to three quarters	score 2
more than three quarters	score 3

The scores from all body regions were also summed to give a total major colour score, with range 0–18.

To examine combinations of colours (predictions 7–9), each species was also scored for the presence or absence of all the following additional colours: brown, red, blue, iridescent-black (when these were not the major colour of the species), and also white, yellow, green and non-iridescent black (for all species).

For analysis, nonparametric tests were used throughout, as the colour scores were not normally distributed.

3. Results

Total scores of major colours differed significantly between the colours (Kruskal-Wallis test, $H_3 = 76.534$, $p < 0.001$). Overall, iridescent-black and blue colours occupied larger total areas of plumage than red and brown (Fig. 1). The series of independent pairwise contrasts confirmed and extended these results, giving significant or near-significant differences for all pairwise colour comparisons (Table 1). The predicted order for extent of uniform areas of coloration was thus generally

Table 1. Pairwise comparisons of major colours in phylogeny-independent contrasts, using Wilcoxon matched pairs tests.

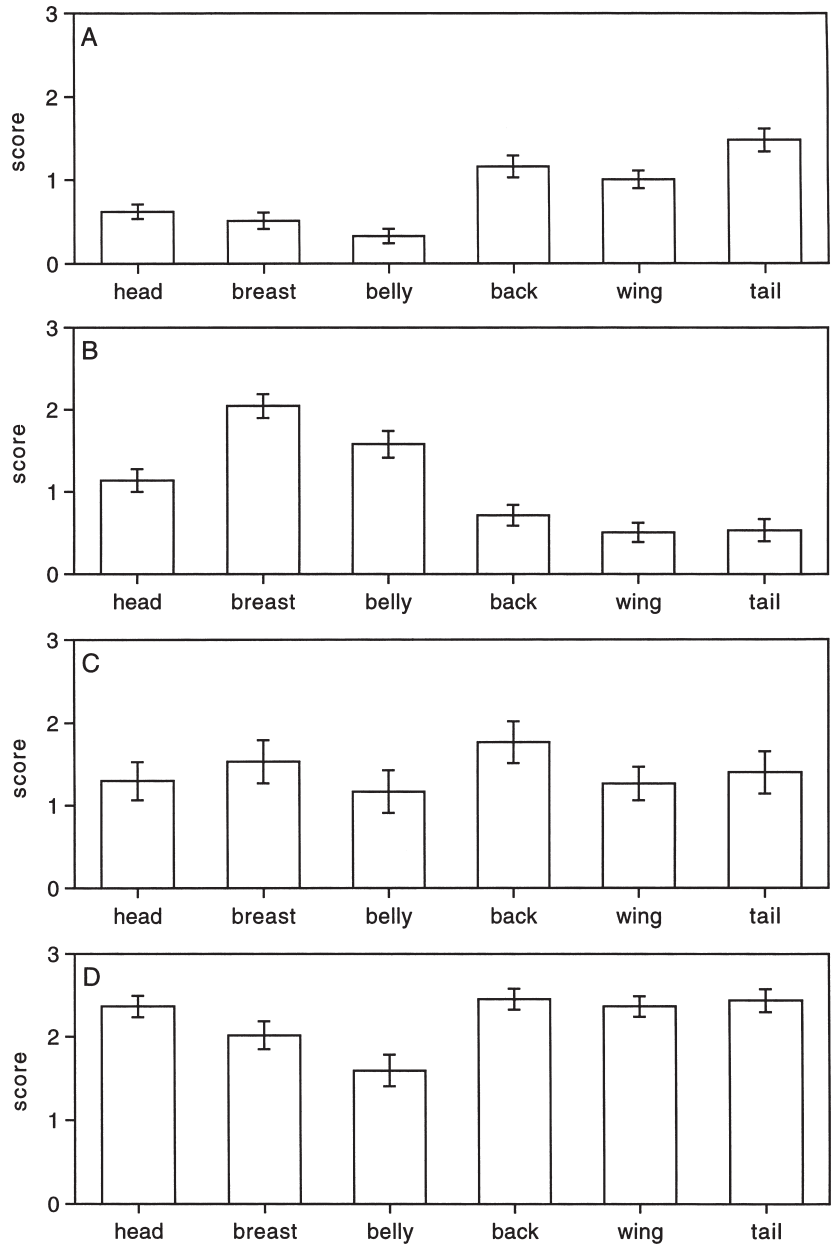| Comparison	*n*	*z*	*p* (1-tailed)	Direction
Brown-red	44	1.705	0.0544	Red > brown
Brown-blue	16	1.566	0.0586	Blue > brown
Brown-iridescent	34	4.919	0.0001	Iridescent > brown
Red-blue	21	1.816	0.0394	Blue > red
Red-iridescent	33	3.850	0.0001	Iridescent > red
Blue-iridescent	17	2.165	0.0059	Iridescent > blue

Fig. 2. Proportion of plumage coloration by major colours on different body regions. Mean ± S.E. colour score shown for each body region for the major colours brown (A), red (B), blue (C), and iridescent-black (D).

confirmed, iridescent-black > blue > red > brown, and predictions 1–5 supported.

The extent of the major colours varied significantly on each body region (Kruskal-Wallis tests, all $H_3 > 52$, $p < 0.001$), and, for all colours except blue, the regions of the body differed in the extent of coloration (Table 2). Brown occupied a greater area on wings, back and tail (Fig. 2A), whereas red was predominant on head, breast and

Table 2. Differences in extent of major colour on body regions — Friedman's tests.

Colour	n	H_5	p (2-tailed)
Brown	108	93.800	0.001
Red	71	90.695	0.001
Blue	30	7.247	> 0.1
Iridescent-black	57	31.186	0.001

belly (Fig. 2B). The extent of blue coloration varied less consistently and not significantly across body regions (Fig. 2C). Iridescent-black, although occurring in large patches on all body regions, was least on the belly and breast (Fig. 2D). Thus, as in prediction 6, the potential indicators of abrasion — iridescent-black and melanin-based plumage — were more extensive dorsally.

The incidence of some additional colours (brown, iridescent-black, white and green) varied significantly with the major colour of the bird (Table 3). Additional brown was more frequent on species with the major colour red (Fig. 3A) and infrequent on iridescent-black birds. Additional iridescent-black was more frequent on birds with the major colours blue and red than brown (Fig. 3D). Brown and iridescent-black plumage were thus relatively infrequently combined in these birds' overall coloration (prediction 7).

Additional blue, although not significantly associated with any major colour (Table 3), occurred least frequently on brown birds (Fig. 3C), as did another plain structural colour, additional green (Fig. 3G), and in this case the incidence of green varied significantly across major colours (Table 3). Additional brown occurred on slightly fewer blue birds than expected (Fig. 3A). Plain structural and melanin-based colours thus generally co-occurred relatively infrequently (prediction 8).

Although a commonly occurring additional colour, white was not randomly distributed with respect to major colour (Table 3), occurring more frequently with brown than with blue and iridescent black (Fig. 3E). This result confirmed the association of brown + white markings as a common colour scheme.

Neither additional red nor yellow differed significantly from a random distribution across major colours (Table 3). Additional brown was most frequent on red birds (Fig. 3A). All structural additional colours — blue, green and iridescent-black — also occurred more frequently on red birds than expected at random (Figs 3C, 3D and 3G). Together, these results indicate an association of carotenoids with all other colour types (prediction 9(i)). Comparing Fig. 3B and Fig. 3F, the two carotenoid-based colours red and yellow were frequently associated with major blue, but differed somewhat in their occurrence with major iridescent-black, and there is thus some hint of a difference between these carotenoid based colours.

Plumage colour schemes involving combinations of red, blue and iridescent-black thus occurred relatively frequently among these birds (prediction 9). Brown melanin-based colour patterns also frequently co-occurred with red, being apparent alternatives to the structural colours as predicted.

Non-iridescent black was a common additional colour and showed no association with any major colour (Table 3, Fig. 3H).

4. Discussion

Overall, the results showed significant support for all the predictions derived from the proposed quality-indicating mechanisms inherent in plain and glossy structural coloration. While other factors, such as directionality of sunlight, crypsis or visibility to predators, might be involved in the positioning of colours, these ultimate factors alone do not seem to be able to explain all aspects of the differential extent, positioning and combination of plumage colours shown here. Quality-indicating signals produced by structural coloration thus seem plausible and warrant further attention.

Structural coloration, if indicating the degree of developmental stability as proposed, acts as an amplifier (Hasson 1989, 1997), increasing the perceptibility of the quality being signalled. This coloration also appears to be a 'revealing indicator' (*sensu* Iwasa *et al*. 1991, Johnstone 1995), having elements of 'honesty by design' (Hasson 1997). The mechanism proposed for glossy structural coloration is an amplifying handicap, making feather quality and abrasion-resistance more

Table 3. Variation in occurrence of each additional colour across the four major colours. *n* gives the number of species (of 266) with each additional colour.

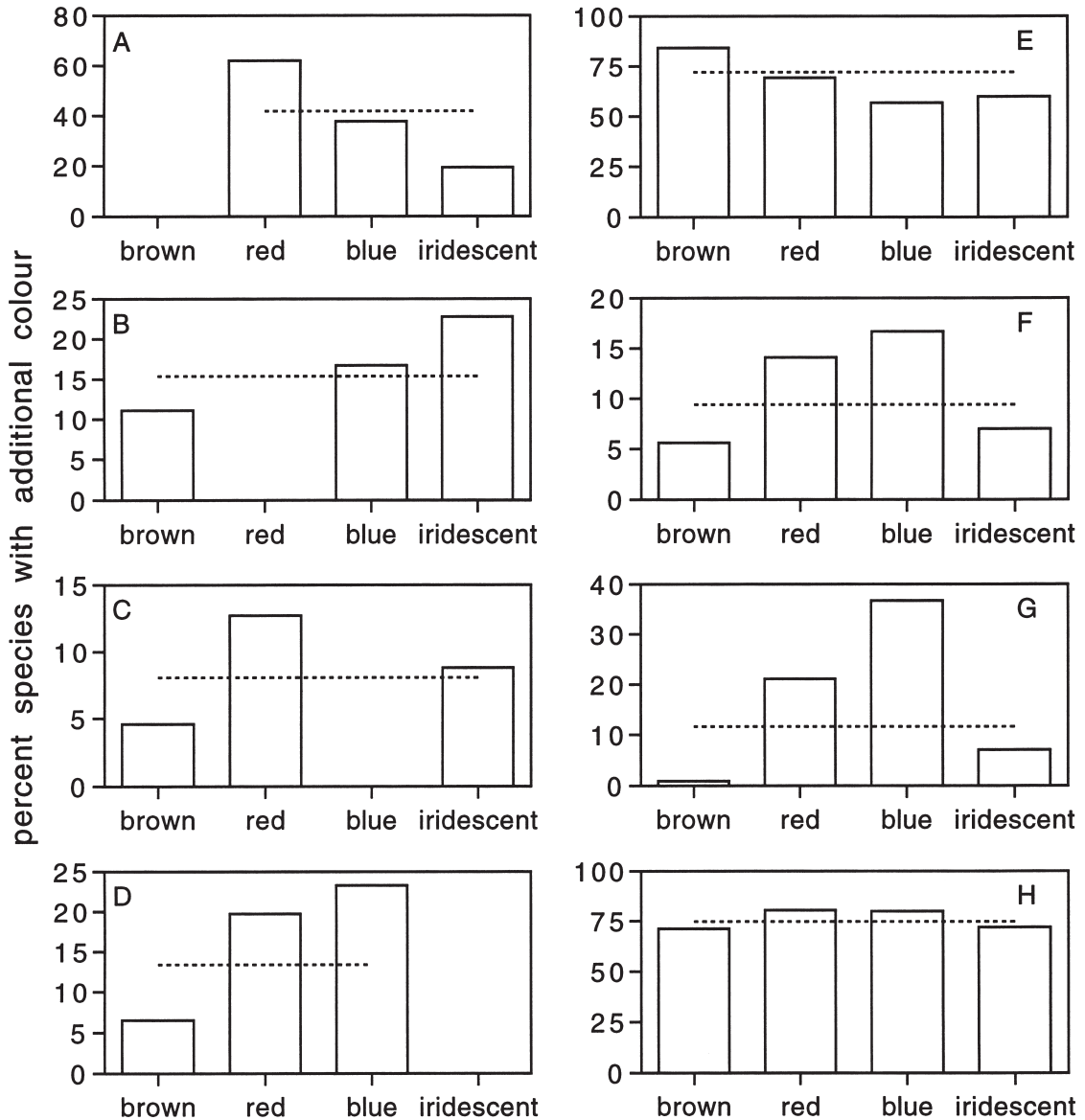| Additional colour	χ^2	df	*p*	*n*
Brown	24.068	2	< 0.0001	66
Red	3.965	2	0.1377	30
Blue	3.799	2	0.1496	19
Iridescent-black	9.450	2	0.0089	28
White	16.103	3	0.0011	191
Yellow	5.945	3	0.1143	25
Green	37.68	3	< 0.0001	31
Black	2.515	3	0.4725	199

Fig. 3. Percentage of species of all major colours also having additional colours present. — A: Additional brown. — B: Additional red. — C: Additional blue. — D: Additional iridescent-black. — E: Additional white. — F: Additional yellow. — G: Additional green. — H: Additional non-iridescent black. Dotted lines show value of random expectation. Species could not have their major colour as an additional colour in A–D.

perceptible while at the same time increasing the likelihood of colour loss due to abrasion. There also appears to be an element of 'honesty by design' inherent in this mechanism. Costs of producing these amplifier signals are thus incurred via the resultant reduction in mating success of poor quality individuals; the costs of the handicap act in addition on the specific quality adver-

tised (feather strength). General costs could include increased predation risk (but see below), however there would appear to be no energetic costs involved. These signals thus seem to have very low costs to high quality individuals.

Plumage coloration potentially provides a signal by which developmental stability can be assessed, independent of and additional to the more

intensely studied but controversial cues involving fluctuating asymmetry (Palmer & Strobeck 1986, Møller & Höglund 1991, Evans & Hatchwell 1993, Graham *et al*. 1993, Møller & Pomiankowski 1993, Møller 1994, 1995, Nilsson 1994, Markow 1995, Leung & Forbes 1997). Alternative possible plumage indicators of developmental stability — regularity and registration of barring patterns (Hasson 1991) as well as the structural coloration mechanism proposed here — suggest the importance of developmental stability as a quality to be assessed. Phenotypic developmental stability, depending on genotype, environment, and their interaction, reveals fitness-related aspects of both the qualities of the individual and of its environment (Leary & Allendorf 1989, Møller 1997, Møller & Swaddle 1997). While the results of this study show the structural coloration mechanism to be plausible, further detailed studies are needed to confirm its occurrence and use as an indicator of quality. In one species, the blue tit *Parus caeruleus*, chroma and brightness of a structural colour influence mate choice (Andersson *et al*. 1998, Hunt *et al*. 1998).

Abrasion-resistance of plumage may be a specific quality which correlates with more general aspects of individual quality, again both phenotypic and potentially genotypic. Plumage requires specific dietary resources as well as energy to produce (Thompson & Boag 1976, Dolnik & Gavrilov 1979, Dietz *et al*. 1992, Murphy & King 1992, Gates *et al*. 1993); poorer or less symmetric feathers are grown by individuals with deficient diets (Grubb 1989, 1991, Swaddle & Witter 1994), and after greater and more costly parental effort (Siikamäki *et al*. 1994, Nilsson & Svensson 1996). Good quality feathers thus may, for example, indicate possession of a good feeding territory during moult, be a 'good parent' indicator (Hoelzer 1989) of the previous breeding attempt, or demonstrate use of a productive migration route for species moulting on staging or wintering grounds, suggesting possession of 'good migration' genes (Fitzpatrick 1994, 1998b). These qualities are complementary to some of the qualities indicated by carotenoid-based colour — health, immunocompetence and parasite resistance, though overlapping as indicators of diet and parental care (Hill 1990, 1991, Johnson *et al*. 1993, Piersma & Jukema 1993, Hill & Montgomerie 1994, Sundberg & Larsson 1994, Dufva & Allander 1995, Sundberg

1995ab, Sundberg & Dixon 1996, Linville *et al*. 1998; but see Seutin 1994). Signals of feather quality could therefore provide information on individual quality different from that conveyed by carotenoid colour. There are few empirical studies of feather quality. Fitzpatrick & Price (1997) showed assortative mating by tail feather quality and a correlation with reproductive success. More work is needed, particularly on the signal roles of markings and structural colours in this respect.

Plumage coloration thus has considerable potential to convey multiple messages, each colour type signalling somewhat different aspects of the quality of the individual and its environment. The associations found here, between carotenoid and both structural and melanin-based colours, suggest the common occurrence of multiple messages being conveyed by plumage coloration. Such multiple messages combining carotenoid colour with colour schemes best positioned dorsally (abrasion-indicating melanin-plus-markings or glossy structural colour) may explain the ventral positioning of red in these birds. Melanin and structural coloration, infrequently occurring together, seem to be alternative signalling systems of similar qualities. Which of these alternative colour schemes a species evolves may depend on other aspects of the signalling environment, e.g., the way in which the quality signal impacts on predatory perceivers of the same plumage coloration.

Conspicuous coloration in some cases reduces the attack rate from predators (Götmark 1993, 1994, 1995, 1997, Götmark & Unger 1994), the coloration being interpreted as constituting a signal of 'unprofitable prey' to the receiving predator (Lyon & Montgomerie 1985). When predators are also avian, it is possible that assessment based on quality-indicating coloration could be used to target poor-quality prey. Both natural and sexual selection may thus coincide to favour signalling of high quality by means of conspicuous coloration. 'Unprofitable prey' signals can be effective only if the signaller itself, while at risk, has a quality-dependent chance of escaping. If the nest of the signaller is at risk of predation instead of or in addition to the signaller, natural selection against parental coloration which reveals the presence of the nest to a predator should result. Nest site and nest predation risk have been correlated with sexual dimorphism in coloration (Johnson 1991, Martin & Badyaev 1996). Risks of nest

predation may thus provide differences in selection pressures which produce a switch between the apparently alternative structural and melanin-plus-markings colour schemes. Quality-indicating colour patterns involving melanin and markings are also largely cryptic, producing a signal to the conspecific which is of a type different from the signal to the predator: conspecifics receive a quality-indicating signal but predators receive a 'cheating', cryptic signal (Hasson 1994) from the same plumage coloration.

This multiplicity of quality-indicating signals inherent in different types of plumage coloration and the indications of 'multiple messages' in plumage colour schemes necessitate a reappraisal of the methods employed in studying plumage coloration. Not only are indices of 'brightness' flawed because of reliance on human visual physiology and by lack of consideration of environmental influences on colour conspicuousness (Endler 1990), but if coloration is not a unitary signal, it cannot be adequately represented on a single scale. Furthermore, 'brightness' plays no part in the quality-indicating function of melanin-plus-markings signals. For glossy structural coloration, the amount of light reflected (brightness *sensu* Endler 1990) is an important part of the signal, but the underlying black colour makes us perceive these birds as 'dull'. Future studies need to measure those aspects of coloration which may convey the quality signal, such as degree of intra-individual uniformity in plain structural colours and interindividual variation in colour uniformity. Separate consideration needs to be given to each type of coloration. There is much work needed to substantiate these proposed quality-signalling mechanisms in plumage coloration; this paper concentrates on ultimate factors rather than proximate mechanisms, sketching a broad outline of possibilities which are crying out for detailed empirical and experimental study.

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Appendix 1. Sources of illustrations for species selection and colour scoring.

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