THE ROYAL SOCIETY

Ultraviolet signals in birds are special

Franziska Hausmann[1], Kathryn E. Arnold[2], N. Justin Marshall[3] and Ian P. F. Owens[4*]

[1]*School of Environmental Sciences, Griffith University, Nathan, Brisbane, Q4111, Australia*
[2]*Division of Environmental and Evolutionary Biology, University of Glasgow, Glasgow G12 8QQ, UK*
[3]*Vision, Touch and Hearing Research Centre, School of Biomedical Sciences, University of Queensland, St Lucia, Brisbane Q4072, Australia*
[4]*Department of Biological Sciences and NERC Centre for Population Biology, Imperial College London, Silwood Park, Ascot SL5 7PY, UK*

Recent behavioural experiments have shown that birds use ultraviolet (UV)-reflective and fluorescent plumage as cues in mate choice. It remains controversial, however, whether such UV signals play a special role in sexual communication, or whether they are part of general plumage coloration. We use a comparative approach to test for a general association between sexual signalling and either UV-reflective or fluorescent plumage. Among the species surveyed, 72% have UV colours and there is a significant positive association between UV reflectance and courtship displays. Among parrots (Psittaciformes), 68% of surveyed species have fluorescent plumage, and again there is a strong positive association between courtship displays and fluorescence. These associations are not artefacts of the plumage used in courtship displays, being generally more 'colourful' because there is no association between display and colours lacking UV reflectance or fluorescence. Equally, these associations are not phylogenetic artefacts because all results remain unchanged when families or genera, rather than species, are used as independent data points. We also find that, in parrots, fluorescent plumage is usually found adjacent to UV-reflective plumage. Using a simple visual model to examine one parrot, the budgerigar *Melopsittacus undulatus*, we show that the juxtaposition of UV-reflective and fluorescent plumage leads to a 25-fold increase in chromatic contrast to the budgerigar's visual system. Taken together, these results suggest that signals based on UV contrast are of special importance in the context of active sexual displays. We review briefly six hypotheses on why this may be the case: suitability for short-range signalling; high contrast with backgrounds; invisibility to predators; exploitation of pre-existing sensory biases; advertisement of feather structure; and amplification of behavioural signals.

Keywords: birds; colour; fluorescence; sexual selection; signalling; ultraviolet reflectance

1. INTRODUCTION

Many bird species possess plumage that reflects ultraviolet (UV) wavelengths. In addition, some species of parrot (Psittaciformes) have fluorescent plumage, which absorbs short wavelengths (UV or blue) and re-emits them at longer wavelengths, making the plumage literally 'glow' (Boles 1990, 1991; Pearn *et al.* 2001; Arnold *et al.* 2002). Parrot species that possess both fluorescent and UV-reflecting plumage often juxtapose these colours. Hence, when viewed by an animal that is sensitive to UV wavelengths, both UV-reflective and fluorescent plumage produce visual contrast in the UV part of the spectrum.

Recent behavioural experiments have shown that birds use both UV-reflective plumage and fluorescent plumage as cues in mate choice (Bennett *et al.* 1996, 1997; Amundsen *et al.* 1997; Andersson & Amundsen 1997; Andersson *et al.* 1998; Johnsen *et al.* 1998; Hunt *et al.* 1998, 1999; Pearn *et al.* 2001; Arnold *et al.* 2002). Debate exists, however, as to whether these signals play a special part in sexual communication or whether they are simply part of general plumage coloration (Goldsmith 1994; Andersson 1996, 2000; Guilford & Harvey 1998;

Owens & Hartley 1998; Sheldon *et al.* 1999; Cuthill *et al.* 2000; Banks 2001; Hunt *et al.* 2001; Arnold *et al.* 2002; Bennett & Owens 2002). A recent experimental study elegantly demonstrated that the UV waveband is not of special importance for mate choice in the zebra finch *Taeniopygia guttata* (Hunt *et al.* 2001). Also, the zebra finch is not, however, a prime candidate for 'special' UV signals because the most important mate-choice cues in this species are song and bill coloration (Burley & Coopersmith 1987; Collins & ten Cate 1996; Banks 2001). The zebra finch does not possess plumage colours with a pronounced UV reflectance peak, its short-wavelength reflection coming from white plumage in which UV reflection is simply a part of broadband reflectance. Here, therefore, we used a comparative approach to test whether there was a general association across many species between UV signals and sexual signalling.

The overall aim of this study was to examine whether interspecific variation in the occurrence of UV signals in birds is associated with interspecific variation in the form of sexual signalling. We asked four questions. First, is UV-reflective plumage non-randomly associated with areas of plumage used in courtship displays? Second, among parrots, is fluorescent plumage non-randomly associated with courtship displays? Third, are areas of plumage that are used in courtship displays generally colourful with respect

*Author for correspondence (i.owens@ic.ac.uk).

Proc. R. Soc. Lond. B (2003) **270**, 61–67
DOI 10.1098/rspb.2002.2200

61

© 2002 The Royal Society

to wavelengths outside the UV part of the spectrum? Finally, what is the visual effect of having fluorescent and UV-reflective plumage regions immediately adjacent to one another?

2. MATERIAL AND METHODS

(a) *Measurement of UV reflectance*

We measured the reflectance spectra of the plumage colours of 108 species of birds. All species were regular breeders on the Australian mainland (Pizzey 1980). All measurements were of adult males. These measurements were performed on museum skins held by the Queensland Museum and on live specimens from Currumbin Sanctuary on the Gold Coast, Australia. Most of these reflectance spectra have been published previously, along with a detailed methodology (Vorobyev *et al.* 1998). We also conducted a study to examine the effects of specimen age on fading in museum samples and found that, although some fading does occur, the main change is a loss of 'chroma' and 'brightness' with little change in 'hue' (Hausmann 1997; McNaught & Owens 2002; J. Marshall, unpublished data; and see Endler (1990) for terminology). In addition, the UV-reflective component of colours does not change differentially relative to the rest of the colour spectrum during fading. We were able to develop, therefore, methods of scoring the presence or absence of UV reflectance and fluorescence that were not affected by fading.

We based our classification of colours on a simplified model of the avian visual system (Vorobyev *et al.* 1998). Birds are known to have a tetrachromatic colour vision system that appears to be extremely conservative (Govardovskii 1983; Vorobyev *et al.* 1998; Hart 2001). In the Passeriformes and Psittaciformes, the four cone types are generally classified as 'UV-sensitive' (UVS), 'short-wavelength sensitive' (SWS), 'medium-wavelength sensitive' (MWS) and 'long-wavelength sensitive' (LWS). In the Anseriformes, Ciconiiformes, Columbiformes and Galliformes, the UVS cone is replaced with a 'violet sensitive' (VS) cone. We therefore based our model on one particularly well-studied avian visual system, that of the budgerigar *Melopsittacus undulates* (figure 1; Bowmaker *et al.* 1997).

Although it is not known exactly how birds process the information received from the four cone types, it is thought that they experience colour by comparing the relative stimulation of different cone types (Osorio *et al.* 1999). Thus, we classified colours on the basis of which of the four cones types they do stimulate versus those that they do not stimulate. Accordingly, we defined 'UV colours' as being those that stimulated the UVS cone but did not stimulate at least one of the other three cone types (i.e. they did not stimulate the SWS cone and/or the MWS cone and/or the LWS cone). Under this definition, all 'UV colours' had a reflection peak in the UV part of the spectrum, and some UV colours also had a second peak elsewhere in the spectrum. 'MW colours' were defined as those that stimulated the MWS cone but did not stimulate the UVS cone. 'LW colours' were defined as those that stimulated the LWS cone but did not stimulate the UVS cone. We were unable to use a corresponding category for 'SW colours' because, in our sample of bird species, there were insufficient colours that stimulated the SWS cone but did not stimulate the UVS cone. MW colours and LW colours were defined as not stimulating the UVS cone because one of the main aims of this study was to compare UV colours with non-UV colours. Our criterion for cone 'stimulation' was that, relative to a white standard, over 20% of light was reflected at

one or more wavelengths within the spectral sensitivity range of a cone class. Our criterion for 'non-stimulation' was that, relative to a white standard, less than 10% of light was reflected at any wavelength within the spectral sensitivity range of a cone class. These are highly conservative criteria based on our knowledge of fading in museum specimens (Hausmann 1997; N. J. Marshall, unpublished data). Cone sensitivities were based on normalized budgerigar cone sensitivities from Bowmaker *et al.* (1997).

Percentage reflectance was measured using an S2000 Ocean Optics spectrometer or the 'Sub-Spec' (Andor Technology/ Oriel) following well-established protocols (Endler 1990; Andersson 1996; Marshall 1996, 2000; Amundsen *et al.* 1997; Andersson & Amundsen 1997; Andersson *et al.* 1998; Johnsen *et al.* 1998; Vorobyev *et al.* 1998; Sheldon *et al.* 1999; Pearn *et al.* 2001; Arnold *et al.* 2002; McNaught & Owens 2002). All measurements were relative to a white 'Spectralon' tablet, and illumination was provided by a xenon flash or a D2000 Ocean Optics combined tungsten/deuterium source. The geometry of sampling was normal to the surface of the plumage area being examined and with illumination held at 45°. Each reading is an average of 10 taken from the same area of plumage or feather, with at least five individuals being measured from each species. For each species, we noted which body regions contained UV colours, MW colours and LW colours, respectively. We used five body regions: (i) head, throat and nape; (ii) chest, flanks belly and vent; (iii) back and rump; (iv) wings; and (v) tail (see Owens & Bennett 1994; Owens & Hartley 1998; Owens & Clegg 1999; Bennett & Owens 2002). We measured all colours in all patches.

(b) *Measurement of fluorescence*

Since fluorescent plumage in birds has only, to our knowledge, been recorded in parrots (Boles 1990, 1991; Pearn *et al.* 2001; Arnold *et al.* 2002), the incidence of fluorescent plumage was assessed by conducting an additional survey of the parrot species held in the skin collection at the Queensland Museum and the Australian Museum, Sydney, encompassing 51 species from 24 genera. Assessment of plumage-area fluorescence was conducted in a completely dark room using an 'RS-Components' hand-held 'blacklight', which had peak emission at 350 nm (see Boles 1990, 1991; Arnold *et al.* 2002). We examined 10 adult males and 10 adult females of each species. We found that fluorescent emission colours included 'red', 'orange', 'yellow' and 'green' (as perceived by the human visual system). Presence or absence of fluorescence was recorded across the five body regions. Fluorescent body regions were classified as any plumage region which, when illuminated with UV-only black-light, emitted light of wavelengths longer than 400 nm. Care was taken not to include fluorescence that resulted from underlying down feathers, which sometimes fluoresce creamy white as viewed through the human visual system. Fluorescent excitation and emission was measured from budgerigar head feathers using a Hitachi F-2000 fluorescence spectrophotometer, demonstrating that the fluorescent emission, in this instance, is caused by short-wavelength excitation peaking close to 350 nm (figure 1*b*). Excitations of other fluorescent feathers are unknown.

(c) *Courtship displays*

We assumed that parts of the plumage that were actively moved during courtship displays were more likely to have a functional role in signalling than areas of plumage not moved during courtship displays. Hence, we collated information from
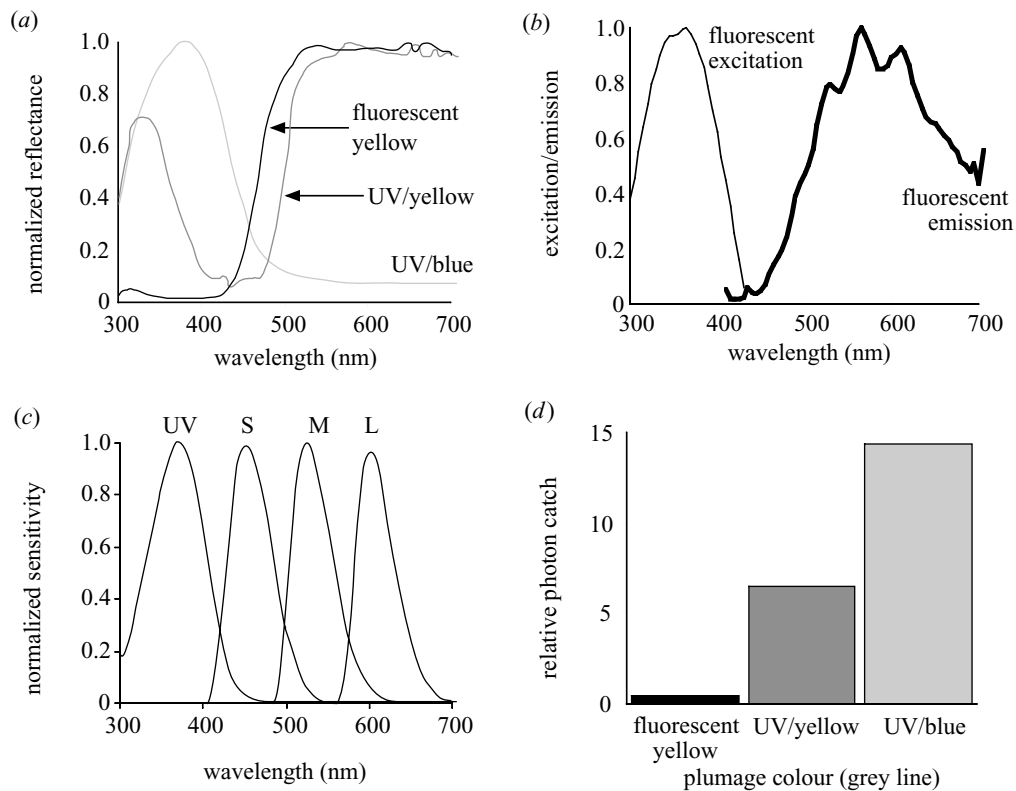
Figure 1. Components used to calculate UV chromatic contrast in budgerigar head colours. (*a*) Normalized reflectance spectra of UV/blue cheek flash (dotted line), fluorescent yellow cheek patch (solid line) and UV/yellow throat patch (grey line). (*b*) Fluorescent characteristics of fluorescent yellow feathers. The thin black line is the fluorescent excitation spectrum. The thick black line is the fluorescent emission spectrum. (*c*) Budgerigar spectral sensitivities (calculated from Bowmaker *et al.* (1997) and Vorobyev *et al.* (1998)). The sensitivity spectrum of each cone type is shown by a black curve. The heavy black curve is the UV spectral sensitivity used in contrast calculations. Cone types are labelled at the top: UV (ultraviolet), S (short), M (medium) and L (long). (*d*) Relative photon catch of UV cone 'looking at' fluorescent yellow cheek patch, UV/yellow throat patch and UV/blue cheek flash, respectively.

the literature on those plumage regions that were reported as being erected, shaken or otherwise actively moved during courtship display (see McNaught & Owens 2002; Bennett & Owens 2002). For each species with either UV colours or fluorescent plumage, we noted which of the five body regions defined above were so used in active courtship displays. Data were collected both from handbooks and monographs (Pizzey 1980; Frith 1982; Serventy 1982; Schodde & Tideman 1986; Boles 1988; Forshaw 1989; Longmore 1991; Johnsguard 1994; Strahn 1994, 1996; Rowley & Russell 1997; Higgins 1999). Body regions not specifically mentioned in the text as being moved were classified as not being involved in the courtship display. We excluded species recorded as having flight displays because it was unclear which body regions might be being displayed.

(d) *Comparative analyses*

When testing for an association between courtship display and a particular form of coloration, the most obvious test to use would be a chi-square test of the proportion of species that used that type of coloration in displayed areas, versus the proportion of species that used that type of coloration in non-displayed areas. Such chi-square tests would be invalid, however, because each species would be counted twice (once in the column describing the colours used in displayed areas and once in the column describing the colours used in non-displayed areas). Hence, to avoid this problem we used binomial tests to test whether particular forms of coloration were more likely than

expected by chance to be associated with sexual signalling. Binomial tests avoid double-counting species because the degrees of freedom are based simply on the number of species contributing to the observed ratio. A separate binomial test was performed for each of the four types of coloration study: UV colour, MW colour, LW colour and fluorescent, respectively. To obtain the 'expected proportion' for each type of colour we first calculated the proportion of species that used that type of coloration in non-displayed body regions. This gave us the null expectation, based on the overall frequency of that particular type of coloration. Second, we calculated the proportion of species that used that type of coloration in displayed body regions. This was the 'observed ratio', based on the frequency with which the colour occurred in courtship regions alone. We then used the binomial tests to find the probability of obtaining the observed ratio, given the expected proportion. The results remain qualitatively unchanged, however, if we use a chi-square test to estimate probabilities or use non-weighted binomial tests with an expected proportion of 0.5.

Comparative tests were initially performed using species as independent data points. However, because closely related species may be more similar than expected by chance (Harvey & Pagel 1991; Bennett & Owens 2002), we subsequently repeated the analysis on higher taxa. Higher-level analysis is a valid method of controlling for phylogenetic non-independence (Harvey & Pagel 1991; Owens 2002). Evolutionarily independent comparisons could not be used because we need to

combine data across plumage regions, whereas tests based on independent contrasts would have to be performed on each region separately. In the case of UV colours, MW colours and LW colours, higher-level analyses were performed on families, selecting one species at random from each family. In the case of fluorescent plumage, which was restricted to the parrot family, higher-level analyses were performed using genera, selecting one species at random from each genus. At no point were tests performed using body regions as independent data points.

(e) *Model of UV chromatic contrast*

Finally, we constructed a simple visual model to calculate the visual effect of juxtaposing UV-reflective and fluorescent plumage, using the budgerigar as a model. The budgerigar possesses a particularly striking example of fluorescent yellow plumage juxtaposed with UV-reflecting blue plumage on the head of both males and females (Pearn *et al*. 2001; Arnold *et al*. 2002) and these head feathers are used in courtship display (Higgins 1999). The juxtaposition of fluorescent and UV-reflective plumage occurs because the yellow feathers on the crown of the head and adjacent to the UV-reflecting UV/blue cheek flashes fluoresce yellow, whereas areas of yellow plumage elsewhere on the head and body do not fluoresce and actually reflect UV wavelengths (these are UV/yellow colours; figure 1*a*). Thus, the UV/blue cheek flashes are effectively surrounded by UV-absorbing fluorescent yellow plumage. To examine possible reasons for this combination, we used available data on the spectral sensitivities of the four single cones in a budgerigar's retina (Bowmaker *et al*. 1997; figure 1*c*), to model the chromatic visual contrast between fluorescent yellow and UV/blue compared with the chromatic contrast of UV/yellow versus UV/blue.

We asked the following question: is there an advantage, in terms of chromatic contrast, to be derived from the UV/blue feathers from being surrounded by fluorescent yellow feathers (as they are in the budgerigar) rather than being surrounded by UV/yellow feathers (which are found elsewhere on the budgerigar)? The relative chromatic contrast (C) of the UV/blue feathers against fluorescent yellow and UV/yellow feathers can be calculated as follows,

$$C = (P_t - P_b)/(P_t + P_b), \qquad (2.1)$$

where P_t is the target photon catch and P_b is the background photon catch (see Vorobyev *et al*. 1998). Photon catches (P) are the relative stimulation of individual cone mechanisms looking at reflective surfaces in the environment and are the sum of the product of the spectral sensitivity (S) multiplied by the photons reflected from the surfaces (R) over a given spectral range or

$$P = \Sigma^{300-700} (S \cdot R). \qquad (2.2)$$

In this instance, we calculate over a broad range of light visible to a budgerigar from 300 to 700 nm but consider only the UV sensitivity of the visual system.

Photons reflected, or radiance from a surface (R) is the product of the wavelengths of illuminating light available in the environment (I) and the reflective characteristics of the surface being examined (X) at each wavelength.

$$R = I \cdot X. \qquad (2.3)$$

A reverse, stepwise combination of equations (2.1–2.3) can be used to estimate object contrast. For simplicity, the illuminant (I) is presumed broadband and flat, that is, plenty of light at all wavelengths known to be true of the open habitats in which

budgerigars display (Endler 1990). For similar calculations, and further explanation, see Endler (1990) and Arnold *et al*. (2002).

The budgerigar has four single cones and the spectral sensitivity of their photoreceptors was calculated from data in Bowmaker *et al*. (1997) (figure 1*c*). Here, we use only the UV cone (see figure 1*c*) for contrast calculations as a way of illustrating the effectiveness of the fluorescent yellow feathers over UV/yellow, in terms of providing chromatic contrast against UV/blue. With relatively few further assumptions, as all four spectral sensitivities are known, it is possible to estimate the discrimination ability of the whole colour vision system (Vorobyev *et al*. 1998). However, such estimates are outside the scope of this paper. This model also ignores the potential role of double cones, which are common in the retinas of many bird species. This was because current evidence suggests that double cones are used in the assessment of overall 'brightness' (and possibly detection of movement and edges) rather than of chroma *per se* (Osorio *et al*. 1999).

3. RESULTS

(a) *UV reflectance*

In common with previous work on birds (e.g. Burkhardt 1989), we found that UV colours in Australian birds are diverse. Among our sample we identified the following subjective categories, based on their appearance through the human visual system: UV/violet, UV/blue, UV/green, UV/yellow, UV/orange, UV/red and UV/white. Out of the 108 species that we surveyed, we found that 72% (78) of species had UV colour plumage in one or more body region, according to our definition of UV colours. Of these 78 species, we were able to find data on the body regions involved in courtship displays for 41 species (visit http:// www/pubs.royalsoc.ac.uk to see electronic appendices to this paper).

Our comparative analyses showed highly significant associations between UV colour and courtship display (table 1*a*). By contrast, there were no significant associations between courtship displays and either MW colours or LW colours (table 1*a*). All of these results remained qualitatively unchanged when the analyses were performed on families (table 1*b*).

(b) *Fluorescence*

Of the 51 parrot species surveyed, 68% (35) had fluorescent plumage, which represented 58% of genera surveyed (14 out of 24). When perceived through the human visual system, the colour of fluorescent emission was variable, including gold-yellow (yellow fluorescence), sulphur yellow (orange fluorescence) and green (green fluorescence).

Of the 35 parrot species in our sample that had fluorescent plumage, we were able to find courtship data for 33. Our subsequent comparative analyses revealed a significant positive association between fluorescent plumage and displayed regions in parrots (table 1*a*), irrespective of whether the analyses were performed on species or genera (table 1*b*). In addition, fluorescent plumage occurred in the same plumage region as UV-reflective plumage in 20 out of the 26 parrot species that we studied that had both fluorescent and UV-reflective plumage.

Table 1. Associations between coloration and courtship displays, using (*a*) species as independent data points, and (*b*) families or genera as independent data points. *n* indicates number of taxa; *p*-values are from two-tailed binomial tests; n.s. is non-significant. (See § 2*a* for details on how colour types were defined.)

| type of coloration | *n* | percentage of taxa with specified coloration | | *p*-value |
		in displayed plumage regions	in non-displayed plumage regions	
(*a*) species-level analyses				
'ultraviolet colours'	41	93	34	<0.0001
'medium-wavelength colours'	41	41	43	n.s.
'long-wavelength colours'	41	32	25	n.s.
fluorescent colours	33	97	46	<0.001
(*b*) family- or genera-level analyses				
'ultraviolet colours'	11	100	9	<0.001
'medium-wavelength colours'	11	42	58	n.s.
'long-wavelength colours'	11	16	25	n.s.
fluorescent colours	14	93	43	<0.01

(c) *Model of UV chromatic contrast*

Using established estimates of relative chromatic contrast, the visual effect of the juxtaposition of fluorescent yellow feathers with UV/blue cheek patches was calculated (see figure 1). For the UV-sensitive mechanism alone (figure 1*c*), the UV chromatic contrast between UV/yellow and UV/blue was only 1.2, whereas the UV chromatic contrast between fluorescent yellow and UV/blue was 30.9 (figure 1*d*). The UV absorptive component of the fluorescent yellow feathers therefore increases the relative contrast with the UV/blue feathers by a factor of 25.7.

4. DISCUSSION

Our results suggest that UV signals are used in a special context by birds. Of the 108 species that we examined in detail, we found that 72% of species had UV-reflective plumage in one or more body region, according to our definition of 'UV colours'. Among these species, UV-reflective plumage was significantly more likely to be found in body regions associated with active courtship displays than expected by chance. Overall, 93% of the species for which we were able to obtain data had UV-reflective plumage in areas used in courtship displays, whereas only 34% of such species had UV-reflective plumage in areas not used in display. This difference is significantly more pronounced than that predicted by chance. The same pattern emerged whether we treated each species as an independent data point or whether we performed our analyses at the family level to control for phylogenetic non-independence. The association with courtship displays also appears unique to UV wavelengths because we found no association between courtship displays and colours that reflected strongly at medium and/or long wavelengths but did not reflect UV light. This shows that the association with courtship is not an artefact of displayed areas being associated with high-contrast colours in general.

Our analysis of fluorescent plumage also provided strong evidence of a link with sexual signalling. We found

fluorescent plumage in 68% (35 out of 51) of the parrot species that we surveyed. In agreement with the prediction of Boles (1990, 1991), we found strong evidence that fluorescent plumage is associated with courtship display in parrots, with more than twice as many species (97%) having fluorescent plumage in displayed areas than have it in non-displayed areas (46%). Again, this difference is significantly more pronounced than expected by chance and remained unchanged even if we used genera, rather than species, as independent data points in the comparative analyses.

Further to our finding that UV-reflective and fluorescent plumage are both found in regions used in courtship displays, we also found that these two forms of plumage are likely to occur in the same body region. These two forms of coloration occurred directly next to each other in 20 of the 26 parrot species that we studied possessing both UV-reflective and fluorescent plumage. Hence, we used a simple model based on the single cone sensitivities and plumage patterns of the budgerigar to quantify the effect of having a UV-reflective blue patch of plumage juxtaposed with a fluorescent patch. This type of plumage arrangement is found on the cheek of the budgerigar. Here, UV-reflective UV/blue feathers are embedded in fluorescent yellow feathers as opposed to being next to the non-fluorescent UV/yellow feathers that occur elsewhere on the head of a budgerigar. Unlike the UV/yellow feathers found elsewhere on the head, the fluorescent yellow feathers absorb rather than reflect UV. Our model suggests that there is an increase in the chromatic contrast for the UV cone 'looking at' the UV/blue cheek patch from a value of 1.2 to 30.9, an increase in excess of 25-fold. We do not know exactly how this difference is interpreted by the budgerigar's colour vision system, but at least in principle this is a significant boost to the efficiency of the UV signal on the head. That the fluorescent signal itself is important for the signalling system and subsequent mate choices has recently been demonstrated (Arnold *et al.* 2002). It is therefore likely that both the fluorescent emis-

sion itself and the contrast caused by the juxtaposition of UV-reflecting and UV-absorbing feathers play a part in signalling (see Hausmann 1997; Pearn *et al.* 2001; Arnold *et al.* 2002).

Why should UV signals in birds be associated with courtship displays? We know of six plausible hypotheses. The first four of these hypotheses are based on the idea that there is something unusually suitable about UV wavelengths for signalling. For instance: (i) UV may be a good medium for signalling over short distances because it is more rapidly degraded over long distances than are longer wavelengths due to particle scatter (Lythgoe 1979; Andersson 1996). Thus, UV signals can be directed at intended receivers while remaining obscure to eavesdroppers. Alternatively, (ii) it has been suggested that UV may constitute a 'secret' avian channel for communication because many potential mammalian predators are unable to perceive UV light (Jacobs 1993; Guilford & Harvey 1998). Equally, (iii) UV signals may be favoured for signalling because they contrast strongly with background foliage. Because chlorophyll absorbs UV wavelengths of light, most plants provide a highly contrasting backdrop to UV-reflective plumage (Andersson *et al.* 1998). Finally (iv) UV signals may have evolved via 'sensory exploitation' to utilize a pre-existing avian preference for UV signals. It has been suggested, for instance, that birds are particularly sensitive to UV wavelengths of light compared with other wavelengths (Burkhardt & Maier 1989) and that birds developed UV vision in order to navigate (see Vos Hzn *et al.* 1994) and/or to find food (see Church *et al.* 1998). In either case, UV signalling would be favoured because birds are predisposed to such signals (Ryan 1990; Endler & Basolo 1998).

The two remaining hypotheses are based on signalling theory. For instance, (v) UV signals may be unusually sensitive indicators of some sort of 'quality'. Many UV-reflective plumage signals are created, in part at least, by the microstructure of the feathers rather than by pigmentation. It has been suggested that structural colours may be unusually good indicators of feather age or feather quality (Prum *et al.* 1994; Fitzpatrick 1998; Andersson 1999; Keyser & Hill 1999, 2000; Prum 1999). Lastly, (vi) UV signals may act as 'amplifiers'. Zahavi & Zahavi (1997) have suggested that many colour patterns exist, not as signals in their own right, but as 'amplifiers' of behaviour. For instance, many UV signals are iridescent. Perhaps such iridescence allows onlookers to judge with greater accuracy the vigour and/or precision of the behaviours involved in courtship display? Further tests are required to estimate the relative importance of these six explanations. The next step is to discover what, if anything, UV signals are signalling.

REFERENCES

Amundsen, T., Forsgren, E. & Hansen, L. T. T. 1997 On the function of female ornaments: male bluethroats prefer colourful females. *Proc. R. Soc. Lond.* B **264**, 1579–1586. (DOI 10.1098/rspb.1997.0220.)

Andersson, S. 1996 Bright ultraviolet colouration in the Asian whistling thrushes (*Myophonus* spp.). *Proc. R. Soc. Lond.* B **263**, 843–848.

Andersson, S. 1999 Morphology of UV reflectance in a whistling thrush: implications for the study of structural colour. *J. Avian Biol.* **30**, 193–204.

Andersson, S. 2000 Efficacy and content of avian colour signals. In *Animal signals: signalling and signal design in animal communication* (ed. Y. Epsmark, T. Amundsen & G. Rosenqvist), pp. 47–60. Trondheim: Tapir Academic.

Andersson, S. & Amundsen, T. 1997 Ultraviolet colour vision and ornamentation in bluethroats. *Proc. R. Soc. Lond.* B **264**, 1587–1591. (DOI 10.1098/rspb.1997.0221.)

Andersson, S., Örnborg, J. & Andersson, M. 1998 Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proc. R. Soc. Lond.* B **265**, 445–450. (DOI 10.1098/rspb.1998.0315.)

Arnold, K. E., Owens, I. P. F. & Marshall, N. J. 2002 Fluorescent sexual signalling in parrots. *Science* **295**, 92.

Banks, A. N. 2001 For your eyes only? The role of UV in mate choice. *Trends Ecol. Evol.* **16**, 473–474.

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Maier, E. S. 1996 Ultraviolet vision and mate choice in zebra finches. *Nature* **380**, 433–435.

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Lunau, K. 1997 Ultraviolet plumage colors predict mate preferences in starlings. *Proc. Natl Acad. Sci. USA* **94**, 8618–8621.

Bennett, P. M. & Owens, I. P. F. 2002 *Evolutionary ecology of birds: mating systems, life histories and extinction*. Oxford University Press.

Boles, W. E. 1988 *Robins and flycatchers of Australia*. Sydney: Angus & Robertson.

Boles, W. E. 1990 Glowing parrots—need for a study of hidden colours. *Birds Int.* **3**, 76–79.

Boles, W. E. 1991 Black light signature for birds? *Aust. Nat. Hist.* **23**, 752.

Bowmaker, J. K., Heath, L. A. & Wilkie, S. E. 1997 Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. *Vis. Res.* **37**, 2183–2194.

Burkhardt, D. 1989 Ultraviolet vision: a bird's eye view of feathers. *J. Comp. Physiol.* A **164**, 787–797.

Burkhardt, D. & Maier, E. J. 1989 The spectral sensitivity of a passerine bird is highest in the UV. *Naturwissenschaften* **76**, 82–83.

Burley, N. & Coopersmith, C. B. 1987 Bill colour preferences of zebra finches. *Ethology* **76**, 133–151.

Church, S. C., Bennett, A. T. D., Cuthill, I. C. & Partridge, J. C. 1998 Ultraviolet cues affect the foraging behaviour of blue tits. *Proc. R. Soc. Lond.* B **265**, 1509–1514. (DOI 10.1098/rspb.1998.0465.)

Collins, S. A. & ten Cate, C. 1996 Does beak colour affect female preference in zebra finches? *Anim. Behav.* **52**, 105–112.

Cuthill, I. C., Partridge, J. C., Bennett, A. T. D., Church, S. C., Hart, N. & Hunt, S. 2000 Ultraviolet vision in birds. *Adv. Stud. Behav.* **29**, 159–214.

Endler, J. A. 1990 On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.* **41**, 315–352.

Endler, J. A. & Basolo, A. L. 1998 Sensory ecology, receiver biases and sexual selection. *Trends Ecol. Evol.* **13**, 415–420.

Fitzpatrick, S. 1998 Colour schemes for birds: structural col-

ouration and signals of quality in feathers. *Ann. Zool. Fenn.* **35**, 67–77.

Forshaw, J. M. 1989 *Parrots of the world*, 3rd edn. Willoughby: Lansdowne Edition.

Frith, H. J. 1982 *Pigeons and doves of Australia*. Adelaide: Rigby Publishers.

Goldsmith, T. H. 1994 Ultraviolet receptors and colour vision: evolutionary implications and dissonance of paradigms. *Vis. Res.* **34**, 1479–1487.

Govardovskii, V. I. 1983 On the role of oil drops in colour vision. *Vis. Res.* **23**, 1739–1740.

Guilford, T. C. & Harvey, P. H. 1998 The purple patch. *Nature* **392**, 867–868.

Hart, N. S. 2001 The visual ecology of avian photoreceptors. *Prog. Retinal Eye Res.* **20**, 675–703.

Harvey, P. H. & Pagel, M. 1991 *The comparative method in evolutionary biology*. Oxford University Press.

Hausmann, F. 1997 Evolutionary ecology of ultra violet reflection and fluorescence in the plumage of birds. Unpublished Hons. thesis. University of Queensland, Australia.

Higgins, P. J. 1999 *Handbook of Australian, New Zealand and Antarctic birds*, vol. 4. Oxford University Press.

Hunt, S., Bennett, A. T. D., Cuthill, I. C. & Griffiths, R. 1998 Blue tits are ultraviolet tits. *Proc. R. Soc. Lond.* B **265**, 451–455. (DOI 10.1098/rspb.1998.0316.)

Hunt, S., Bennett, A. T. D., Cuthill, I. C. & Griffiths, R. 1999 Preferences for ultraviolet partners in the blue tit. *Anim. Behav.* **58**, 809–815.

Hunt, S., Cuthill, I. C., Bennett, A. T. D., Church, S. C. & Partridge, J. C. 2001 Is the UV waveband a special communication channel in avian mate choice? *J. Exp. Biol.* **204**, 2499–2507.

Jacobs, G. H. 1993 The distribution and nature of colour vision among the mammals. *Biol. Rev.* **68**, 413–471.

Johnsen, A., Andersson, T., Örnborg, J. & Lifjeld, J. T. 1998 Ultraviolet plumage ornamentation affects social mate choice and sperm competition in blue throats (Aves: *Luscinia s. svecica*): a field experiment. *Proc. R. Soc. Lond.* B **265**, 1313–1318. (DOI 10.1098/rspb.1998.0435.)

Johnsguard, P. A. 1994 *Arena birds: sexual selection and behaviour*. London: Smithsonian Institution Press.

Keyser, A. J. & Hill, G. E. 1999 Condition-dependent variation in the blue-ultraviolet colouration of structurally based plumage ornament. *Proc. R. Soc. Lond.* B **266**, 771–777. (DOI 10.1098/rspb.1999.0704.)

Keyser, A. J. & Hill, G. E. 2000 Structurally based plumage colouration is an honest signal of quality in male blue grosbeaks. *Behav. Ecol.* **11**, 202–209.

Longmore, W. (ed.) 1991 *Honeyeaters and their allies of Australia*. Sydney: Angus & Robertson.

Lythgoe, J. N. 1979 *The ecology of vision*. Oxford: Clarendon Press.

McNaught, M. & Owens, I. P. F. 2002 Interspecific variation in plumage colour among birds: species isolation or light environment? *J. Evol. Biol.* **15**, 505–514.

Marshall, N. J. 1996 Measuring colours around a coral reef. *Biophot. Int* **Jul.–Aug.**, 52–56.

Marshall, N. J. 2000 The visual ecology of reef fish colours. In *Animal signals. Signalling and signal design in animal communication* (ed. Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 59–96. Trondheim: Tapir Academic.

Osorio, D., Miklósi, A. & Gonda, Z. 1999 Visual ecology and perception of coloration patterns by domestic chicks. *Evol. Ecol.* **13**, 673–689.

Owens, I. P. F. 2002 Male-only care and classical polyandry in birds: phylogeny, ecology and sex differences in remating opportunities. *Phil. Trans. R. Soc. Lond.* B **357**, 283–293. (DOI 10.1098/rstb.2001.0929.)

Owens, I. P. F. & Bennett, P. M. 1994 Mortality costs of parental care and sexual dimorphism among birds. *Proc. R. Soc. Lond.* B **257**, 1–8.

Owens, I. P. F. & Clegg, S. M. 1999 Species-specific sexual plumage: species-isolating mechanisms or sexually selected ornaments? *Proc. 22nd Int. Ornithol. Congr. Durban*, pp. 1141–1153.

Owens, I. P. F. & Hartley, I. R. 1998 Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proc. R. Soc. Lond.* B **265**, 397–407. (DOI 10.1098/rspb.1998.0308.)

Pearn, S. M., Bennett, A. T. D. & Cuthill, I. C. 2001 Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulates*. *Proc. R. Soc. Lond.* B **268**, 2273–2279. (DOI 10.1098/rspb.2001.1813.)

Pizzey, G. 1980 *A field guide to birds of Australia*. Sydney: Angus & Robertson.

Prum, R. O. 1999 Development and evolutionary origin of feathers. *J. Exp. Zool.* **285**, 291–306.

Prum, R. O., Morrison, R. L. & Teneyck, G. R. 1994 Structural colour production by constructive reflection from ordered collagen arrays in a bird. *J. Morphological* **222**, 61–72.

Rowley, I. & Russell, E. 1997 *The fairy wrens*. Oxford University Press.

Ryan, M. J. 1990 Sexual selection, sensory systems and sensory exploitation. *Ox. Surv. Evol. Biol.* **7**, 157–195.

Schodde, R. & Tideman, S. C. (eds) 1986 *Readers' digest complete book of Australian birds*. Sydney: Readers Digest.

Serventy, V. N. (ed.) 1982 *The wrens and warblers of Australia*. Sydney: Angus & Robertson.

Sheldon, B. C., Andersson, S., Griffith, S. C., Örnborg, J. & Sendecka, J. 1999 Ultraviolet colour variation influences blue tit sex ratios. *Nature* **402**, 874–877.

Strahn, R. (ed.) 1994 *Cuckoos, nightbirds and kingfishers of Australia*. Sydney: Angus & Robertson.

Strahn, R. (ed.) 1996 *Finches, bowerbirds and other passerines of Australia*. Sydney: Angus & Robertson.

Vorobyev, M., Osorio, D., Bennett, A. T. D., Marshall, N. J. & Cuthill, I. C. 1998 Tetrachromy, oil droplets and bird plumage colours. *J. Comp. Physiol.* A **183**, 621–633.

Vos Hzn, J. J., Coemans, M. A. J. M. & Nuboer, J. F. W. 1994 The photopic sensitivity of the yellow field of the pigeon's retina to ultraviolet light. *Vis. Res.* **34**, 1419–1425.

Zahavi, A. & Zahavi, A. 1997 *The handicap principle*. Oxford University Press.