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Ultraviolet reflectance by the cere of raptors

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Ultraviolet (UV) signals have been shown to play key roles in social and sexual signalling in birds. Using a spectrophotometer, we analysed the colour of the cere (skin above the beak) of a diurnal raptor, the Montagu's harrier (*Circus pygargus*), and show that it reflects in the UV part of the spectrum. The cere is a well-known sexual signal in raptors, with carotenoid based pigmentation being indicative of quality. We thus hypothesized that UV reflectance also signals quality. Accordingly, we found that in our sample of wild males, the location of the UV peak was related to the orangeness of cere and correlated with male body mass and condition (mass corrected for size). Also, males with brighter UV were mated to females that laid earlier, as expected if UV reflectance relates to a male's quality and attractiveness. Future studies should investigate the relationships between UV reflectance and carotenoid pigmentation of cere, and test how UV reflectance influences mate choice.

Keywords: colour; sexual signal; *Circus pygargus*; ultraviolet vision; mate choice

1. INTRODUCTION

Many animals exhibit brightly coloured traits that function in intra-sexual competition and mate choice (e.g. Andersson 1994). In birds, carotenoid- or melanin-based signals (e.g. Badyaev & Hill 2000; Møller *et al.* 2000) and structural plumage coloration (e.g. Andersson 1999; Keyser & Hill 1999) have received particular attention. Experiments have also shown that many species detect near-ultraviolet light (UV; 300–400 nm) in addition to the spectrum visible to humans (400–700 nm; Cuthill *et al.* 2000) and can use UV signals for quality appraisal and mate choice (e.g. Bennett *et al.* 1996; Johnsen *et al.* 1998; Hunt *et al.* 1999). The emphasis so far has been on UV reflectance by plumage traits, but there is growing evidence that beaks, skin or soft sexual ornaments reflect in the near UV (e.g. Jourdie *et al.* 2004; Dresp *et al.* 2005). However, the functions of UV reflectance by fleshy ornaments and the mechanisms underlying quality signalling remain barely known.

Carotenoids determine the red, yellow and orange colour of many secondary sexual characters, such as fleshy ornaments and colourful plumage, which are among the most familiar targets of female choice (Hill 2002). Animals cannot synthesize carotenoids but must ingest them with their food, and ultimately carotenoid intake limits ornament expression (Olson & Owens 1998; Hill *et al.* 2002). Carotenoids are not only deposited in ornaments, they are also important antioxidants and powerful immunostimulants (Møller *et al.* 2000). Thus, competition for the available pool of carotenoids between ornaments and immune function may confer honesty on sexual signals (von Schantz *et al.* 1999). Recent studies have suggested links between carotenoid based coloration and plumage (structural) UV reflectance, because carotenoid spectra often exhibit a secondary reflectance peak in the near-UV wavelengths (Burkhardt 1989; Bleiweiss 2004, 2005). Many non-plumage features with UV reflectance are also carotenoid-based ornaments, like the gape of passerine nestlings (Jourdie *et al.* 2004), the combs of grouse (Mougeot *et al.* 2005) or the yellow or orange beak of zebra finches (Bennett *et al.* 1996), blackbirds (Bright & Waas 2002) and mallards (Peters *et al.* 2004). Thus, UV and carotenoid based signals might not be independent.

The cere of raptors (skin surrounding the nostrils and beak; figure 1*a*) is typically yellow–orange and a carotenoid-based signal of individual quality (Bortolotti *et al.* 2000, 2003). In this paper, we report on a bimodal pattern of reflectance by the cere of a semi-colonial raptor, Montagu's harrier *Circus pygargus*, with a marked peak in the UV, and another in the yellow–orange part (500–600 nm) of the spectrum. We then tested whether the UV reflectance and 'orangeness' of cere were related and might play a role in sexual signalling. Sexual signals are expected to be condition-dependent (e.g. Andersson 1994), so we investigated whether cere reflectance was related to male body mass and condition (mass corrected for size). We also investigated how cere reflectance varied with laying date. We expected males that were more attractive and of higher phenotypic quality to be mated with females that lay earlier in the breeding season, either because they were more attractive and paired earlier or because they attracted females of higher quality.

2. MATERIAL AND METHODS

(a) *Captures*

We conducted the study in 1999 in western France (Marais de Rochefort and south of Deux Sèvres). Males were captured using pole-traps during the prelaying period (April–May). We caught and measured 19 males, but measured cere colour only from nine. All males were mature (i.e. greater than 2 years old). We measured (tarsus length, wing length, body mass) and wing-tagged all birds. Neither trapping nor wing-tagging had any effect on breeding success, and all males resumed normal breeding behaviour after release. Laying date was estimated directly if nests were visited during laying, or by backdating from hatching date estimated from body measurements of nestlings. We determined laying date for 8 of the 9 males in which cere colour was measured (the remaining was a non-breeder).

(b) *Colour measurements*

We measured spectral reflection of the cere in the range 300–700 nm using a spectrophotometer. Measurements were done at the capture sites. The cere was subjected to a deuterium–halogen light source (DH2000, Top Sensor System) with a spectral range from 280 to 800 nm and the reflected light transferred to the spectrophotometer (S2000). The light source illuminated the cere through an optic fibre (FCR-7UV200-2-45 ME), which was inserted in a plastic 'pen' that allowed elimination of ambient light during measurement once this was correctly placed under the light spot. The pen was placed perpendicularly to the sample, so the light reached the sample perpendicularly. Another optic fibre

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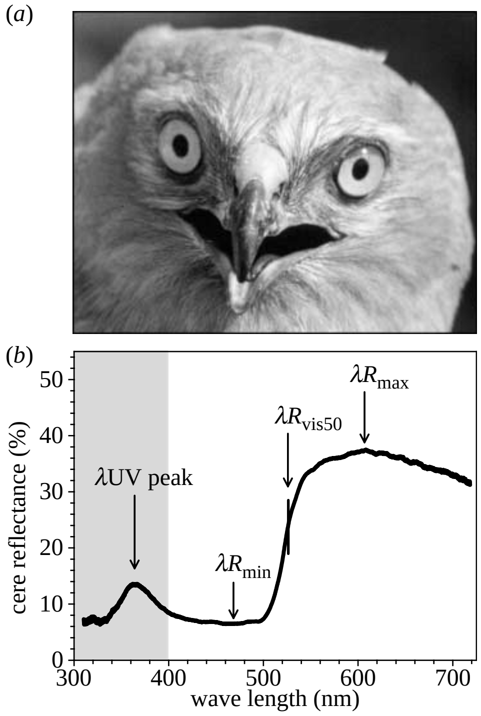

Figure 1. (*a*) Portrait of a male Montagu's harrier showing the cere (skin area above the beak, in between the eyes); (*b*) Reflectance pattern of a male cere in the spectrum range 300–700 nm. The grey area represents the near-UV.

collected the reflected light and transferred it to the spectrometer. We converted the data into digital information using a DAQ Card 700 and calculated reflectance data relative to a white reference tile (WS-2) and to the dark using Spectrawin 3.1 software. Both references were kept clean and protected by a cover that was removed only briefly for taking reference measurements. The software gave a value for the black and white references and the sample data at each 0.4 nm interval between 300 and 700 nm, enabling us to calculate the percentage reflectance at each interval point.

(c) *Colour variables*

We summarized cere reflectance data by calculating the following colour variables (see Endler 1990): (i) total brightness (total reflectance in the interval 300–700 nm); (ii) UV chroma (reflectance in the interval 300–400 nm/total brightness, in percentage); (iii) yellow chroma (reflectance in the interval 500–600 nm/total brightness, in percentage); (iv) λUV peak (wavelength, λ, at which maximal reflectance is reached in the UV; 300–400 nm); $\lambda R_{\mathrm{vis50}}$, as the spectral location of the reflectance band at long visible wavelengths (so-called 'cut-off' wavelength) was estimated as the value midway ($\lambda R_{\mathrm{vis50}}$) between that of minimum (λR_{min}) and maximum (λR_{max}) reflectance (figure 1*b*; Pryke *et al.* 2001; Bleiweiss 2004). $\lambda R_{\mathrm{vis50}}$ values are indicative of the yellowness/orangeness of cere (higher values, more orange cere).

(d) *Statistical analyses*

We used SAS 8.01 for all analyses. We investigated the relationships between reflectance variables and male body mass or laying date, using Spearman correlations. We included sampling date as a partial variable in all correlation analyses. Using data from all captured males, we established that body mass was positively related to wing length ($F_{1,17}=5.97$, $p<0.05$, $R^2=21.6\%$) but not to tarsus length ($F_{1,17}=0.30$, $p=0.58$, $R^2=0.0\%$). When looking at the relationship between colour variables and condition (mass corrected for size), we thus corrected for wing length as an index of size, by including it as a partial variable in the correlation analyses.

3. RESULTS

Reflectance of cere increased in the range 500–600 nm (figure 1*b*), which is the yellow/orange part of the colour spectrum. Reflectance also showed a marked peak in the UV part of the spectrum (300–400 nm; figure 1*b*). Descriptive statistics of cere colour variables (means ± s.d.) were as follows: total brightness: 28 698 ± 11 760; UV chroma: 12.52 ± 1.78%; yellow chroma: 32.75 ± 2.41%; λUV peak: 365.9 ± 3.1 nm; $\lambda R_{\mathrm{vis50}}$: 552.5 ± 9.3 nm. λUV peak and $\lambda R_{\mathrm{vis50}}$ were positively correlated ($R_s=0.68$; $p<0.05$), and greater total brightness was associated with greater UV chroma ($R_s=0.63$; $p=0.07$) but no other significant correlations were found between colour variables (all $p>0.25$).

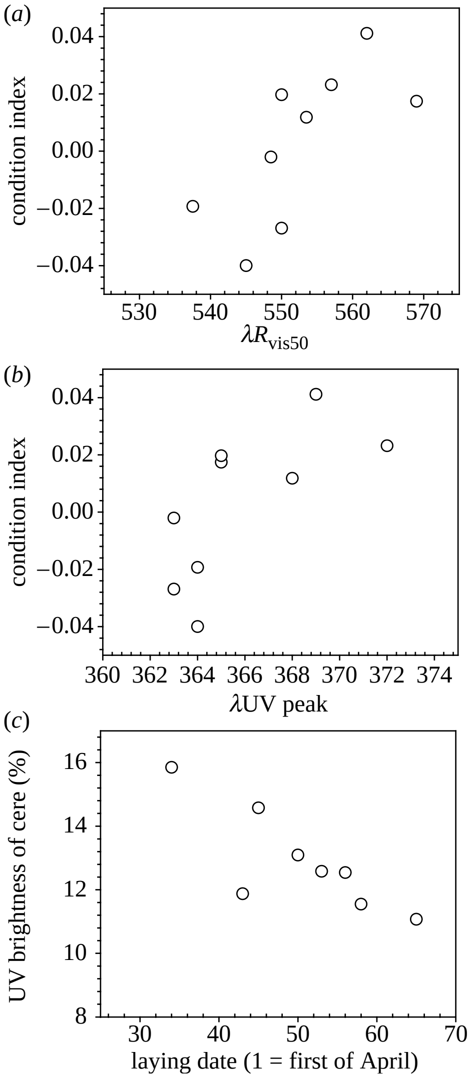

Figure 2. Relationships between male condition index (weight corrected for wing length) and (*a*) $\lambda R_{\mathrm{vis50}}$ and (*b*) UV hue ($n=9$ males). (*c*) Relationship between UV brightness of male cere and laying date of pairs ($n=8$ males).

Variation in male body mass was not significantly related to total brightness, UV chroma or yellow chroma ($R_s=0.10$, 0.12 and 0.13, respectively; all $p>0.73$; $n=9$) but positively correlated with λUV peak ($R_s=0.78$; $p<0.05$) and $\lambda R_{\mathrm{vis50}}$ ($R_s=0.70$; $p<0.05$). When including wing length as a partial, body mass was also not significantly related to total brightness, UV chroma or yellow chroma (all $p>0.79$), but positively correlated with λUV peak ($R_s=0.87$; $p<0.01$) and $\lambda R_{\mathrm{vis50}}$ ($R_s=74$; $p<0.05$). Thus, heavier males, in better condition, had a UV peak at greater wavelength and more orange/red cere than lighter males, in poorer condition (figure 2*a*,*b*).

Laying date was not significantly related to yellow chroma, λUV peak or λR_{vis50} ($R_s = -0.31$, -0.20 and -0.21, respectively; all $p > 0.46$; $n = 8$), but males with greater total brightness ($R_s = -0.81$; $p < 0.05$) and UV chroma ($R_s = -0.76$; $p < 0.05$; figure 2*c*) were from pairs that laid earlier in the season. The male that did not pair (non-breeder) had the lowest cere brightness and UV chroma (10.0%).

4. DISCUSSION

We showed for the first time that the cere of a raptor reflects in the UV. In contrast, the reflectance of grey back feathers or of black primaries, measured at the same time as cere and with the same spectrophotometer, did not show such a peak in the UV (F. Mougeot and B. E. Arroyo 1999, unpublished work). The reflectance pattern of the cere resembled that recently described for other soft parts of birds (see Jourdie *et al.* 2004; Mougeot *et al.* 2005). There is increasing evidence that UV signals play key roles in sexual signalling in birds (Cuthill *et al.* 2000), with females preferring males with brighter UV signals (e.g. Bennett *et al.* 1996; Johnsen *et al.* 1998). Cere visible colour is known as a quality sexual signal in raptors (e.g. Bortolotti *et al.* 2003), and its UV reflectance might influence signal perception. Below we discuss the significance of our findings, with particular emphasis on: (i) UV vision capability by raptors, and a possible role of UV in sexual signalling and (ii) potential mechanisms underlining quality signalling and links between UV reflectance and carotenoid pigmentation of the cere.

Experiments have shown that at least two raptor species, the Eurasian kestrel *Falco tinnunculus* and rough-legged buzzard *Buteo lagopus*, both specialist predator of voles, possess UV vision and use it for foraging and detecting vole scent marks (Viitala *et al.* 1995; Honkavaara *et al.* 2002). The Montagu's harrier is also specialized on vole predation and could therefore possess UV vision and use it for foraging. In the saker falcon *Falco cherrug*, recent work showed that UV reflectance by the white wash at nest sites relates to breeding success and might function a signal of quality (Potapov & Sale 2005). Although it remains to be tested for Montagu's harrier, this evidence indicates that several raptors possess UV vision. More work is needed to establish whether UV vision is widespread in raptors, which could be done by experiments, or by investigating whether species possess UV sensitive retinal pigment and a UV-transmitting ocular media (see Hart & Vorobyev 2005).

In Montagu's harriers, the location of the UV peak and the yellow–orangeness (λR_{vis50}) of the cere were related to each other and to the male's body mass and condition. In raptors, visible cere colour (yellow–orangeness) varies with diet, differs between sexes (e.g. Negro *et al.* 1998; McDonald 2003), and is a carotenoid-based signal of quality (e.g. Bortolotti *et al.* 2003). Our results are consistent with previous findings that birds in better condition have greater carotenoid pigmentation, and a more orange cere (Bortolotti *et al.* 2003). Carotenoid spectra often exhibit a secondary reflectance peak in the near-UV wavelengths (Burkhardt 1989; Bleiweiss 2004) visible to most birds but not to normal humans. Both the visible and UV reflectance bands result from a strong absorption band over short visible wavelengths (400–500 nm), which can create a bimodal profile pattern of reflectance (Bleiweiss 2005), as seen in the cere of Montagu's harrier (figure 1*b*). Indeed, chemists use absorptive properties to analyse carotenoids because the atomic structure and concentration of the carotenoid molecules determine the shape and prominence of the absorption band in a very precise way. Thus, omitting UV wavelengths ignores the physical mechanism by which carotenoids produce or influence colour, as well as how birds may perceive these pigments (Bleiweiss 2004, 2005).

Males with a brighter cere and greater UV reflectance were from pairs that bred earlier, which suggests that they were of higher quality (Newton 1979). Laying earlier in the breeding season is also associated with a better breeding success in harriers (see Arroyo *et al.* 2004) and other raptors (e.g. Newton 1979). The male with least UV brightness was one that failed to pair and breed. In Montagu's harrier, mate fidelity is very low (*ca* 14%) and older, more experienced females, lay earlier than others (Arroyo *et al.* 2004). Males with brighter UV ceres might thus have paired faster and/or with females of higher quality. In most raptors, males feed their mate during most of the breeding cycle, and in particular during the pre-laying period (e.g. Newton 1979). Laying date depends to some extent on the amount of food provided by the male during the pre-laying period (Arroyo *et al.* 2004), so males with brighter UV might also have been better food providers, resulting in earlier breeding. Laying date and condition were related to different colour variables, suggesting that attractiveness is not (at least solely) based on condition.

Despite our small sample size, our correlative results support our hypothesis that cere reflectance, and UV reflectance in particular, has a quality revealing function. They also suggest a link between UV and carotenoid-based signalling, which has implications for the honesty of the signal (von Schantz *et al.* 1999). Our data and colour measurements were from wild raptors and made in the field, which is both valuable and a limitation. Because our sample size was small and our results are correlative, we cannot be too conclusive, but this work should lead to more studies on UV signalling in wild and captive raptors. Whether UV signals are of special importance for bird mate choice has been advocated and criticized (Hunt *et al.* 2001; Hausmann *et al.* 2003), but the role of the UV waveband should be considered in conjunction with the rest of the avian visible spectrum (Hunt *et al.* 2001). Future studies should further investigate the relationships between UV reflectance and carotenoid pigmentation of fleshy ornaments and test a possible role of UV vision in mate choice in raptors.

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