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The role of ultraviolet-A reflectance and ultraviolet-A induced fluorescence in the appearance of budgerigar plumage: insights from spectrofluorometry and reflectance spectrophotometry

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Fluorescence has so far been found in 52 parrot species when illuminated with ultraviolet-A (UVA) 'black' lamps, and two attempts have been made to determine whether such fluorescence plays any role in sexual signalling. However, the contribution of the reflectance versus fluorescence to the total radiance from feathers, even in the most studied species to date (budgerigars), is unclear. Nor has the plumage of this study species been systematically assessed to determine the distribution of fluorescent patches. We therefore used spectrofluorometry to determine which areas of budgerigars fluoresce and the excitation and emission spectra involved; this is the first time that such a technique has been applied to avian plumage. We found that both the yellow crown and (normally hidden) white downy chest feathers exhibit strong UVA-induced fluorescence, with peak emissions at 527 nm and 436 nm, respectively. Conversely, the bright-green chest and dark-blue tail feathers do not fluoresce. When comparing reflectance spectra (400–700 nm) from the yellow crown using illuminants with a proportion of UVA comparable to daylight, and illuminants with all UVA removed, no measurable difference resulting from fluorescence was found. This suggests that under normal daylight the contribution of fluorescence to radiance is probably trivial. Furthermore, these spectra revealed that males had fluorescent crowns with substantially higher reflectance than those of females, in both the UV waveband and at longer wavelengths. Reflectance spectrophotometry was also performed on a number of live wild-type male budgerigars to investigate the chromatic contrast between the different plumage areas. This showed that many plumage regions are highly UV-reflective. Overall our results suggest that rapid surveys using UVA black lamps may overestimate the contribution of fluorescence to plumage coloration, and that any signalling role of fluorescence emissions, at least from the yellow crown of budgerigars, may not be as important as previously thought.

Keywords: parrot; budgerigar; fluorescence; ultraviolet; reflectance spectrophotometry; spectrofluorometry

1. INTRODUCTION

If an ultraviolet-A (UVA) emitting 'black' lamp is shone on some species of parrot, certain plumage areas fluoresce visibly to humans (Boles 1991). That is, UV radiation is absorbed and then re-emitted at longer, human-visible, wavelengths (Mazel 1991). Völker (1937) was one of the first to describe this phenomenon, noting fluorescing plumage areas in 52 parrot species, mostly Australian genera. Avian fluorescence has so far been found only in parrots; it seems to originate from a rare yellow pigment whose structure is as yet unknown (Völker 1937; Durrer 1986; Boles 1991), although see Stradi *et al.* (2001) for identification of the red pigments in *Ara macao*.

UV-induced fluorescence should not be confused with UV reflection from plumage, which has been shown to be used in mate choice in the five passerine species so far tested (reviewed by Cuthill *et al.* 2000) and also the budgerigar (Pearn *et al.* 2001), a small sexually dimorphic monogamous member of the parrot family that lives throughout the arid zones of inland Australia (Juniper & Parr 1998). Whether fluorescence is involved in parrot mate choice, however, remains unclear: the only published behavioural experiments (Pearn *et al.* 2001; Arnold *et al.* 2002) reach different conclusions, using the same species, budgerigars.

It should be borne in mind that the vividly fluorescing plumage colours observed in darkness, under artificially intense UV black lights, as in Völker (1937), Boles (1991) and Arnold *et al.* (2002), may be visually irrelevant under normal daylight; i.e. they may not have a biologically significant signalling role. This is a reasonable null hypothesis because a great many substances can be made to fluoresce under black lamps, e.g. rocks and minerals and a multitude of compounds and molecules derived from plants and animals, yet these have no known signalling role.

So far, fluorescence in parrot plumage has been identified mostly by this technique of shining black lamps on specimens, and noting which regions fluoresce. Black lamps emit primarily at *ca.* 365 nm, but have a broad emission of UVA wavelengths, even extending slightly into

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the human visible range (which is why they appear a deep violet to humans). However, studies to date have not indicated the narrow wavelength range that induces fluorescence (the excitation spectrum), nor how such excitation might vary between regions or species. Similarly, they have not indicated the spectrum of emitted light from this narrow-band illumination (the emission spectrum). Such data, to our knowledge, have not been published for the budgerigar, nor for any other parrot species. Hence, our goal was to quantify fluorescence more accurately, using (i) reflectance spectrophotometry in the 300–700 nm range (i.e. UV-VIS) and (ii) spectrofluorometry, with budgerigars as a model species. From such data, better estimates of the contribution of fluorescence to plumage radiance under less-artificial lighting conditions can be made.

2. METHODS

(a) *Reflectance spectrophotometry of male budgerigar plumage regions*

We measured a number of plumage and body regions of five male live wild-type budgerigars, of approximately the same age, obtained from several breeders. The regions were illuminated at 45° to the surface using a Zeiss CLX 500 xenon lamp. Reflected light was collected at 90° to the surface, and the spectrum determined with a Zeiss MC 500 UV-VIS spectrophotometer.

The feathers were positioned parallel to the source of illumination and collection, and illuminated from the proximal end. Reflectance was measured relative to a 99% Spectralon white standard, at a wavelength range of 300–700 nm. Four measurements were taken from random locations within each region, reference measurements were taken between each region and between each bird, and the reflectance standard was cleaned and cross-checked against a virgin standard prior to the study.

(b) *Spectrofluorometry of male budgerigar plumage regions*

We used a FluoroMax-2 spectrofluorometer in combination with DataMax software (Instruments SA, Inc., Jobin Yvon/Spex Division, NJ, USA). The illuminant was a 150 W continuous ozone-free xenon lamp, with a beam-splitter directing one portion of the light onto a reference photodiode (to allow continuous correction for variations in light intensity as a function of wavelength) and the other portion onto the sample. Only emission scans were run, which involve setting a series of fixed excitation wavelengths from which all emitted wavelengths in the given range are measured. In total, four regions of plumage were sampled, using feathers from the yellow crown, green chest, blue tail and white downy chest plumage of dead wild-type captive-bred male birds, frozen at −20 °C since death. In addition, a blank (black mount only) and a fluorescent yellow adhesive label were used as controls and checks. All samples were mounted on a matt black mount consisting of pieces of Perspex cut to fit snugly in the cuvette holder of the front-face accessory. Owing to the time-intensive nature of the measurements, only males were measured.

Each emission scan was run at increments of 1 nm, with an integration time of 0.5 s. Slit widths were set to 0.5 mm (2.14 nm bandpass) as the signal was intense and exceeded 4×10^6 counts per second (cps). The individual scans were each 10 nm apart between the excitation wavelengths of 320 nm and 680 nm, with the upper limit of radiance collection set at 700 nm (the approximate upper limit of avian vision). The wavelength at which the scans started was always 15 nm above the excitation wavelength, to minimize detection of reflectance, as, in feathers that have mixtures of reflecting and fluorescing compounds, there may be artefactual peaks of strong reflectance at wavelengths close to those being used for excitation. However, there will still be an anomalous peak in the first few scans of the emission spectra, caused by some scatter, at approximately double the excitation wavelength.

When obvious fluorescent peaks were detected from plumage regions, we ran an additional set of narrower-interval scans to determine the exact excitation wavelength at which the peak of fluorescence occurred. For example, if the greatest fluorescence was found at an excitation wavelength of 360 nm, 21 scans were run, each 1 nm apart as opposed to 10 nm apart, between 350 nm and 370 nm (with the emission-scan increment remaining at 1 nm).

(c) *Reflectance spectrophotometry of male and female budgerigar crown feathers*

We measured the crowns of five male and five female, live, wild-type budgerigars of approximately the same age, obtained from several breeders. Measurements were taken with the geometry and equipment described in § 2a.

The emission spectrum of a xenon lamp is a closer approximation to that of natural sunlight than most commercially available sources. This is one reason why it is often the illuminant of choice in UV-VIS spectrophotometry. Consequently, to simulate the contribution of UVA-induced fluorescence to the total radiance from a sample when under natural illumination, we used a xenon source and two treatments, the order of which was randomized. In the first, a 5 cm × 5 cm single-thickness UV blocking Perspex filter (see Pearn *et al.* (2001) for transmission spectra) was positioned in a fixed location in the incident light beam, perpendicular to the beam and at 45° to the base plate. Under these conditions there can be no UV-induced fluorescence and so the measured radiance is 'pure' reflectance. In the second treatment, there was no filter in the incident light beam, allowing the full complement of wavelengths to illuminate the subject's crown and potentially excite fluorescence. Each bird was measured under both conditions, and 10 measurements were taken per condition from random locations within each crown, to reduce any experimental error.

Male–female and treatment differences in the data at 527 nm (the fluorescent yellow crown emission peak, see § 3b) and 365 nm (the fluorescent yellow crown excitation/absorption peak, see § 3b) were analysed by balanced repeated-measures analyses of variance (ANOVA).

3. RESULTS

(a) *Reflectance spectrophotometry of male budgerigar plumage regions*

The spectra from a sample of plumage regions are displayed in figure 1*a*(i–iii). The values in table 1 detail the reflectance peaks or, for step-function spectra, 'wavelengths of maximum slope'; these spectral parameters correlate well with perceived colour (Endler 1990; Bradbury & Vehrencamp 1998). Those plumage regions not included in the graphs are the black and yellow barred or scalloped head and back feathers, which consist of black bars interspersed with UV-reflecting yellow (similar to the barred wing), and the black cheeks (a uniform flat black).

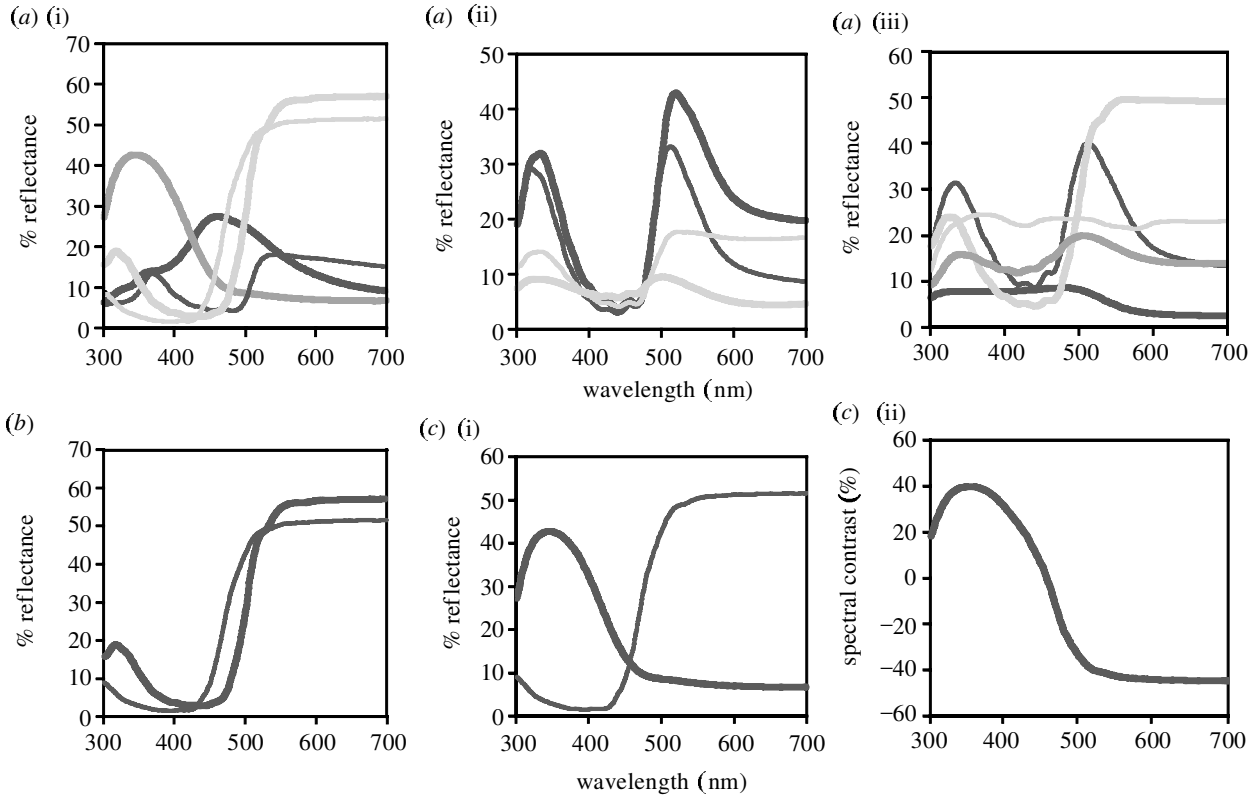

Figure 1. Reflectance spectrophotometry results from live wild-type male budgerigars. (*a*) Reflectance spectra of (i) the plumage regions of the head and face (thick dark-grey line, blue cere; thick mid-grey line, blue cheek patch; thin dark-grey line, upper mandible; thick light-grey line, yellow cheeks; thin light-grey line, yellow crown); (ii) some of the plumage regions from the body (thick dark-grey line, green chest; thin dark-grey line, green rump; thick light-grey line, green primaries; thin light-grey line, black and yellow barred wing) and (iii) the plumage regions from the tail area (thick dark-grey line, blue tail; thin dark-grey line, turquoise undertail; thick light-grey line, yellow undertail; thin light-grey line, legs; thick mid-grey line, green undertail coverts). (*b*) A comparison between the reflectance spectra of a UV-absorbing and fluorescing yellow pigment (thin grey line, crown) and a UV-reflecting yellow pigment (thick grey line, cheeks). (*c*)(i) A comparison between the reflectance spectra of the fluorescent yellow crown (thin grey line) and the UV-blue cheek patches (thick grey line), and (ii) spectral contrast between the fluorescent yellow crown and the UV-blue cheek patches.

It can be seen from the figures and the table that the majority of the remaining plumage is highly UV reflecting, with UV-yellows, UV-greens and UV-blues, and many of these spectra contain separate UV peaks.

Figure 1*b* demonstrates the difference between a UV-absorbing fluorescent yellow patch (the crown) and a UV-reflecting yellow patch (the cheeks). The UV-yellow not only has a considerably higher intensity of UV reflection, but also seems to be brighter at longer wavelengths. Interestingly, the wavelengths of maximum slope (see table 1) differ by 35 nm, indicating that they are likely to be perceived as different hues by a bird.

Figure 1*c*(i,ii) describes the contrast between two adjacent patches on the head and face of the budgerigar: a fluorescent yellow patch (in this case the crown) and a UV-blue cheek patch. Figure 1*c*(i) illustrates the reflectance spectra of these two samples, and it is apparent from the graph that there is considerable variation between the patches both in the short UV-blue waveband (360–410 nm) and in the longer yellow waveband (>500 nm). This is demonstrated more clearly in figure 1*c*(ii), a contrast spectrum, where the reflectance values for the fluorescent yellow crown have been subtracted from the values for the UV-blue cheek spot.

Other facial regions that may generate strong chromatic contrasts include the fleshy blue cere, which lacks a peak in the UV but has a relatively strong blue peak at 463 nm, and the upper mandible, a yellowish keratin-based structure, which has both a UV peak at 370 nm and a green–yellow peak at 544 nm.

(b) *Spectrofluorometry of male budgerigar plumage regions*

The green chest (figure 2*b*) and blue tail (figure 2*c*) of the male budgerigar have negligible fluorescence. They are comparable to the black 'blank' sample (figure 2*f*). Conversely, figure 2*e* shows extremely intense yellow fluorescence from a fluorescent yellow adhesive label (the positive control). Although only *ca.* 10% of the intensity of this positive control, there is considerable fluorescence from both the crown and downy feathers of the plumage (figure 2*a*,*d*, respectively). More-detailed sets of excitation and emission spectra (figure 3) clarify the characteristics of this fluorescence.

The yellow crown of the budgerigar fluoresces in the yellow region of the human visible spectrum (figure 2*a*): maximum fluorescence excitation is at 365 nm (akin to the emissions of a UV black lamp); maximum fluorescence emission is at 527 nm; and the maximum intensity is *ca.* 9×10^6 counts s^{-1} (see figure 3*a*). The white downy fea-

Table 1. The reflectance peaks and 'wavelengths of maximum slope' of reflectance spectra (300–700 nm) from five live male budgerigars.
(An asterisk denotes a wavelength of maximum slope. All peaks are above 10% except those enclosed within brackets.)

plumage region	UV peak (nm)	other peak (nm)
yellow crown	—	468*
yellow cheeks	318	503*
blue cheek patches	348	—
blue cere	—	463
upper mandible	370	544
green chest	333	520
green rump	321	512
green primaries	(328)	503
barred wing	333	480*
blue tail	(338)	(478)
green undertail coverts	343	507
yellow undertail	328	503*
turquoise undertail	333	512
contrast peaks	350	700

thers (figure 2*d*), some of which are situated beneath the green chest contour feathers of the bird, while others form the base of these feathers, fluoresce in the violet region of the human visible spectrum: maximum fluorescence excitation is at 375 nm, still in the UVA waveband; maximum fluorescence emission is at 435 nm; and the maximum intensity is *ca.* 23×10^6 counts s^{-1} (see figure 3*b*). Extrapolated excitation spectra, obtained by selecting the series of excitation values at which the emission peak occurs (either 527 nm (crown) or 435 nm (downy feathers)) from every 10 nm emission scan, can be seen as filled squares in figure 3*a*,*b*.

(c) *Reflectance spectrophotometry of male and female budgerigar crown feathers*

There are negligible differences in the shapes of the spectra between 400 and 700 nm when measured with and without UV in the illuminant (figure 4). If UVA wavelengths are removed from the incident light beam with UV blocking filters, then fluorescence cannot be excited. If they remain, then some fluorescence can occur. Hence, the presence of any fluorescence under these conditions would appear as a difference in shape between the spectra: an additional peak would be visible in the UV+ spectrum, centred around the emission maximum of 527 nm. However, a balanced ANOVA carried out at 527 nm showed no hint of an effect of treatment ($F_{1,8} = 0.02$; $p = 0.882$). There was, however, a high degree of sexual dimorphism in this part of the spectrum, with males being significantly brighter than females ($F_{1,8} = 10.01$; $p = 0.013$). No sex × treatment interaction occurs ($p > 0.5$).

ANOVA was also carried out at 365 nm, the peak absorbance/excitation wavelength of yellow crown fluorescence. This value is close to 371 nm, the peak sensitivity of the budgerigar's UV-sensitive retinal cone (Bowmaker *et al.* 1997). The data were transformed to normalize the ANOVA residuals using the Box–Cox procedure to determine the best possible power (in this case −0.337) by which to transform the values. There was a significant effect of sex ($F_{1,8} = 8.81$; $p = 0.018$), with males being brighter than females at this wavelength, and a highly significant effect of treatment ($F_{1,8} = 2881.52$; $p < 0.001$), with the UV+ treatment being much brighter than the UV− treatment. There was no sex × treatment interaction ($p > 0.25$).

4. DISCUSSION

This study primarily comprises, for the first time, a series of quantitative fluorescence emission and excitation spectra from a variety of plumage regions of the male budgerigar. Neither the UV-reflecting blue tail nor the green chest of the male budgerigar showed evidence of fluorescence. As expected, the crown exhibited clear yellow fluorescence. This peaked at 527 nm and was maximally excited by illumination at 365 nm, the same wavelength at which the UV black lights emit.

Perhaps most importantly, however, our results reveal that the white downy feathers situated beneath the non-fluorescent green chest feathers exhibit strong violet fluorescence, peaking at 435 nm. This was maximally excited by light at 375 nm, again in the UVA waveband. This finding reinforces our caution when drawing conclusions about any signalling role played by fluorescence. First, we have evidence that down feathers are strongly fluorescent, yet they are not normally visible on the exterior of the bird, so are probably not involved in signalling. Second, violet fluorescing down feathers have also been observed on domestic turkey chicks between 1 and 22 days of age (Sherwin & Devereux 1999). By the time they are adults and sexual selection takes place, this fluorescence disappears from view, most probably because it is covered by non-fluorescent feathers. Third, the presence of such non-visible fluorescent feathers suggests that not all fluorescence is costly, and it cannot be assumed that all such patches have a visual signalling role, or one that is involved in sexual selection. This contradicts the assertion in Arnold *et al.* (2002) that the elaborate biochemical pathways that produce fluorescence (Stradi *et al.* 2001) imply that it may be costly and therefore an honest indicator of individual quality.

These results also highlight the need for extreme caution when conducting rapid surveys of fluorescence in museum specimens using black lamps. It is possible that in some cases the fluorescence noted from particular colour patches on a specimen could have originated from the downy feathers beneath the patch as opposed to the surface-feather pigments themselves. Unlike wild birds, it is quite common for museum specimens to have ruffled plumage, hence unnaturally revealing the down beneath (S. M. Pearn, personal observation).

The latter parts of this study have also shown that, in conditions approximating daylight in the relative contribution of UVA, the fluorescence we have characterized is, in fact, undetectable at its emitted yellow wavelengths. Our analysis had a high power (83.1%) to detect even a modest increase in radiance of 5%, so we can be confident that the contribution of fluorescence is very low under these lighting conditions. No artificial light source perfectly matches the irradiance spectrum of daylight, but the xenon arc used in the latter part of this study has a similar proportion of different wavebands to bright sunlight, including the UV.

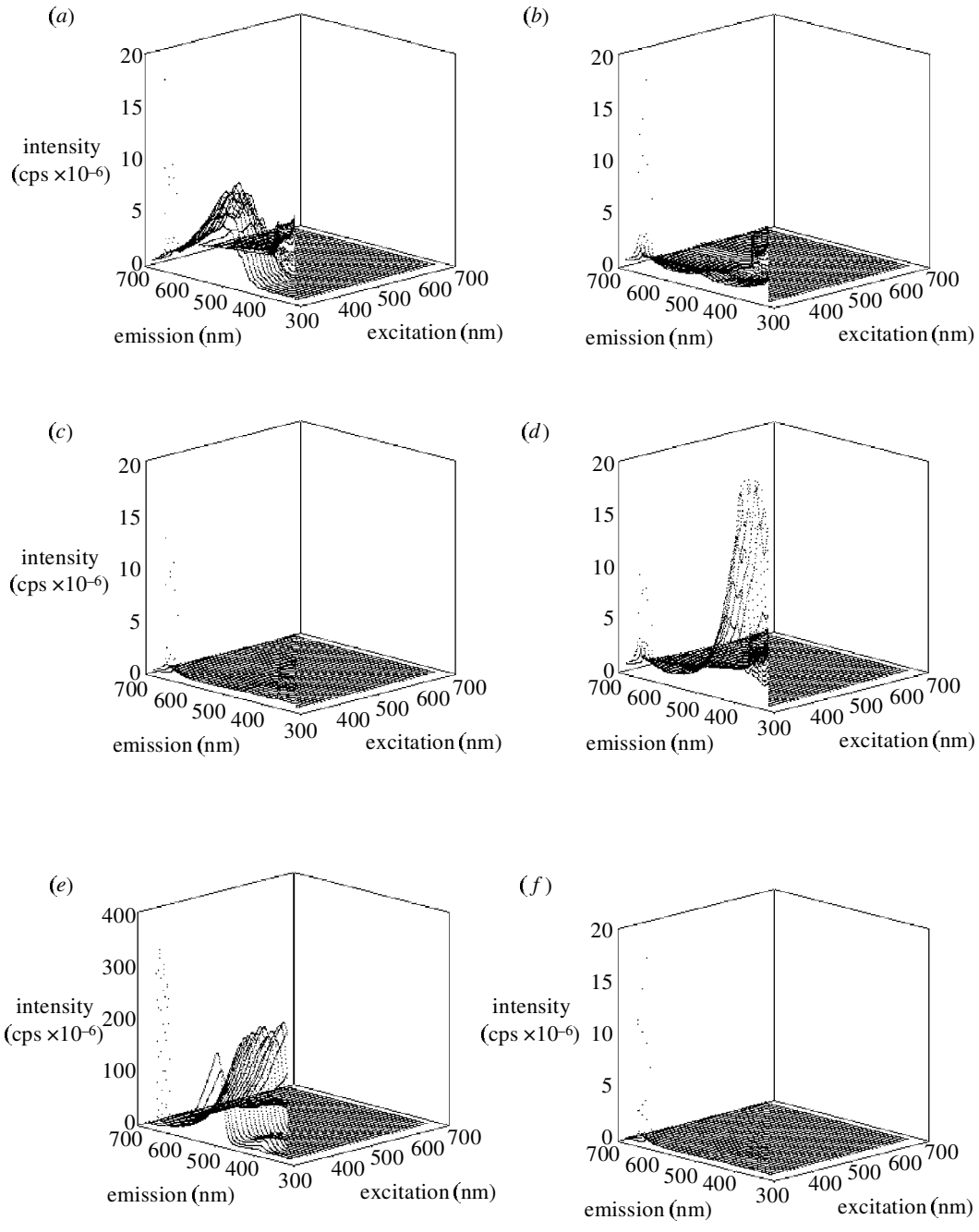

Figure 2. (*a–f*) Three-dimensional representations of a series of spectrofluorometry emission spectra from six samples: (*a*) budgerigar crown (male); (*b*) budgerigar chest (male); (*c*) budgerigar tail (male); (*d*) budgerigar downy feathers (male); (*e*) fluorescent paper; and (*f*) blank.

Such findings shed doubt on the importance of long-wavelength fluorescence emissions in parrot coloration. The lack of any significant difference between treatments at the point at which fluorescence would occur implies that if there is any signalling role played by fluorescence it may not be the enhancement of the brightness of the yellow region of the spectrum that is involved, but instead the absorption of ultraviolet wavelengths (Pearn *et al.* 2001; Arnold *et al.* 2002). This also disagrees with the findings of Arnold *et al.* (2002), who calculated that fluorescent plumage adds 14% extra 'chromatic signal' to the crown of this species. Indeed, the outcome of our spectrophotometry measurements demonstrates that the non-fluorescent yellow of the cheeks has higher reflectance at long wavelengths than the fluorescent yellow crown, which rather suggests that fluorescence is not an adaptation for boosting longwave radiance (i.e. making a more saturated yellow).

We do, however, believe that it is important that plumage patches with UVA absorption seem frequently to occur next to patches with UVA reflectance; this would tend to increase within-body contrast in the UVA region of the spectrum. We have shown that the occurrence of fluorescent yellow feathers around the UV-reflecting violet cheek patch of the budgerigar results in high levels of contrast in the UV waveband as well as at longer, yellow, wavelengths.

As a final point, our spectrophotometry measurements also showed that males have a considerably brighter crown than females, despite fluorescence being undetectable. This

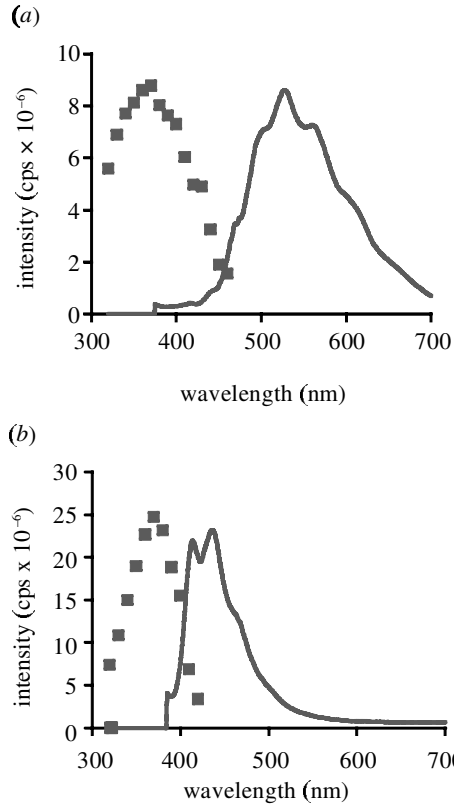

Figure 3. The shapes of the emission spectra (solid lines) and extrapolated excitation spectra (filled squares) where the fluorescence is at its greatest intensity for (*a*) the male crown (maximum emission *ca.* 9×10^6 counts s^{-1}) and (*b*) the male downy feathers (maximum emission *ca.* 23×10^6 counts s^{-1}).

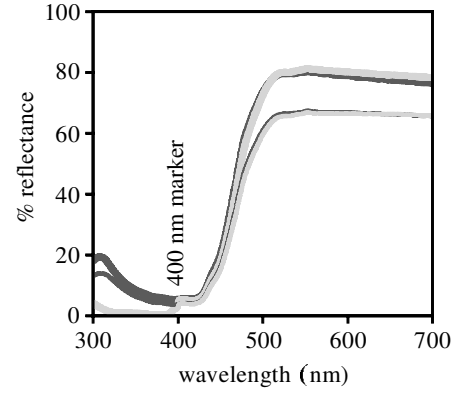

Figure 4. The average reflectance spectra from the male (thick lines) and female (thin lines) budgerigars in both treatments. UV– treatments (light grey lines) are those where the UV blocking filter was in place. These spectra have been adjusted (balanced) at each point between the 400 nm marker and 700 nm by a proportion equivalent to the decrease in quantal flux caused by the UV blocking filter i.e. 'crown reflectance under UV− treatment' divided by 'UV blocking filter transmission at the same wavelength $\lambda/100$'. UV+ treatments (dark grey lines) are those without a filter in place. (Thick dark-grey line, unmanipulated male (UV+); thick light-grey line, UV– male (balanced); thin dark-grey line, unmanipulated female (UV+); thin light-grey line, UV– female (balanced)).

additional brightness appears to occur across the avian visible spectrum, in both the UV waveband and at longer wavelengths. This is the first indication that this species is more sexually dichromatic than previously thought: male–female differences are not determined by cere colour alone. Not only are males a brighter yellow, but interestingly there is also hidden sexual dimorphism in the UV-reflective component of the fluorescent yellow crown.

Moreover, this result reveals that fluorescent plumage patches do not absorb all the UV irradiance. There is a portion that is reflected, not absorbed, and this portion is sexually dichromatic. This is an important finding as it has implications for previous and future mate-choice experiments. As we have shown (Pearn *et al.* 2001), manipulation of UV wavelengths has a strong impact on female mate choice in budgerigars, which means it is essential that when manipulating fluorescence, one does not also manipulate UV reflectance, as confounding effects may appear. While manipulations via filters, as used in Pearn *et al.* (2001), are able to separate these effects, it is probable that application of UV-absorbing sunblock to fluorescing plumage, as used in Arnold *et al.* (2002), will eliminate this UV-reflective component of the plumage patch, which could thereby induce unintentional effects of UV reflection on female choice.

In conclusion, although fluorescence has been recorded in 52 of the *ca.* 350 species of parrot (Völker 1937; Juniper & Parr 1998), in our view, there is as yet no clear evidence that it plays a sexual signalling role, or a signalling role in any other context. Given the evolutionary isolation of parrots, it is possible that fluorescence in some parrot plumage may not be an adaptation for signalling, but rather an epiphenomenon of the evolution of different pigment types in this unusual family. The widespread existence of fluorescent plumage in hidden downy feathers, which we report here, certainly does not suggest that it is costly to produce, or even that it will always be visible to other birds.

Note added in proof. During the referee process, we discovered that a paper on a similar topic had been submitted to *Proceedings* series B. Hausmann, F., Arnold, K. E., Marshall, N. J. & Owens, I. P. F. 2003 Ultraviolet signals in birds are special. *Proc. R. Soc. Lond.* B **270**, 61–67. (DOI 10.1098/rspb.2002.2200.)

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