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Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*

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As in many parrots, the plumage of the budgerigar *Melopsittacus undulatus* reflects near-ultraviolet (UVA) wavelengths (300–400 nm) and exhibits UVA-induced fluorescence. However, there have, to our knowledge, been no tests of whether the yellow fluorescence observed under intense UVA illumination has any role in signalling. Four experiments were carried out on wild-type budgerigars, where the presence and absence of UV reflectance and fluorescence were manipulated using filters. Few studies have attempted to separate the contribution of UV reflectance to plumage hue as opposed to brightness or distinguish between a role in sexual as opposed to social preferences. However, our first experiments show that not only do females consistently prefer UV-reflecting males, but also that the observed preferences are due to removal of UV affecting the perceived hue rather than brightness. Furthermore, we found no effect of the light environment on male response to females, suggesting that the female preferences relate to plumage colour *per se*. Whilst UV reflectance appears important in heterosexual choice by females, it has no detectable influence on same-sex association preferences. The results from the second series of experiments suggest that enhancement of the budgerigar's yellow coloration through fluorescence has no effect on male attractiveness. However, the fluorescent plumage may play a role in signalling by virtue of the fact that it absorbs UVA and so increases contrast with nearby UV-reflecting plumage. Our study provides convincing evidence that UV reflectances can play a role in mate choice in non-passerines, but no evidence that the yellow fluorescence observed under UVA illumination is itself important as a signal.

Keywords: ultraviolet vision; fluorescence; mate choice; avian vision; colour vision; budgerigar

1. INTRODUCTION

Unlike humans, many birds have ocular media that are transparent to near-ultraviolet (UVA) wavelengths (*ca.* 315–400 nm) and a fourth single cone type that is sensitive to UV (Bowmaker *et al.* 1997). Birds are thus generally thought to be tetrachromatic (Burkhardt 1989; Bennett *et al.* 1994; Bowmaker *et al.* 1997; Vorobyev *et al.* 1998; Osorio *et al.* 1999*a*,*b*; Cuthill *et al.* 2000*a*,*b*). As perception of colour depends crucially on the photoreceptor spectral sensitivities and neural processing of the receiver (Endler 1990), it is clearly unwise to make judgements about the colours that signal to birds based on human colour perception (Endler 1990; Bennett *et al.* 1994).

Birds frequently have remarkable and conspicuous colour patterns and recent research has shown that many plumage patches include UV reflection (Burkhardt 1989; Burkhardt & Finger 1991; Finger *et al.* 1992; Finger & Burkhardt 1994; Bennett *et al.* 1996, 1997; Andersson *et al.* 1998; Hunt *et al.* 1998; Andersson 1999; Cuthill *et al.* 1999; Langmore & Bennett 1999). This UV reflection has been shown to be involved in mate choice in a few passerines, therefore suggesting that UV reflection is a sexually selected component of their plumage, with female assessment of the males preferentially occurring in the presence of UV information (reviewed by Cuthill *et al.* 2000*a*). However, whilst such studies provide necessary evidence, they are not always sufficient for proving that UV colours are important in mate choice. First, the effects of the removal of UV on both hue and brightness need to be separated. Second, choice needs to be shown to relate to heterosexual preferences rather than it being a non-specific response to any conspecific or even to arbitrary complex visual stimuli or the light environment itself. Only one published study, to our knowledge, fulfils all these criteria (Bennett *et al.* 1996), so it is perhaps premature to assume that UV wavelengths have widespread importance in avian colour-based mate choice when the direct evidence is actually rather limited.

The parrot family has another interesting aspect to its coloration: fluorescence. Fluorescence occurs when short wavelength light is absorbed and then re-emitted at longer wavelengths (Mazel 1991); in parrots, absorption is in the UVA waveband and re-emission is in the human visible spectrum. Volker (1937) was the first to report avian fluorescence, having found a yellow fluorescent pigment in the feathers of several varieties of Australian parrots, including white cockatoos (genus *Cacatua*), various rosellas (genus *Platycercus*), blue winged parrots (genus *Neophema*) and the budgerigar *Melopsittacus undulatus*. This phenomenon was described in more detail by Boles (1991), who shone a UV 'black light' (peak emission within the UVA waveband at 365 nm) on museum specimens and recorded the presence or absence of a resulting fluorescent 'glow', i.e. long-wavelength fluorescent emissions. He found that the fluorescence occurred in either yellow feathers such as the crown of the budgerigar or in green feathers where yellow pigments combine with blue structural colours, such as in *Neophema* species (Boles 1991). This phenomenon has been mentioned surprisingly infrequently (Volker 1937; Dyck 1971; Boles 1991), and its influence in relation to avian signalling has, to our knowledge, never been studied. Fluorescence may be involved in signalling in two not necessarily mutually exclusive ways. First, the emission may supplement the long-wave reflectance in order to produce more intense and saturated radiance (parrot

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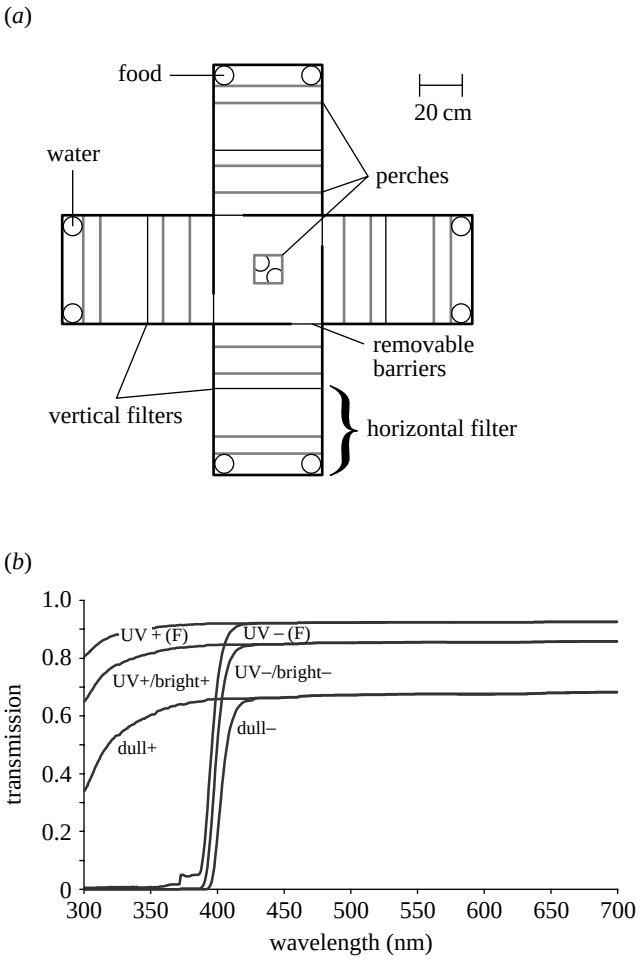

Figure 1. (*a*) Scale view of the mate choice apparatus. (*b*) Transmission spectra of the six filter types used in these experiments (adapted from Bennett *et al*. 1996). The spectra are the means of five randomly located measurements taken with a Unicam Prism spectrophotometer (now Thermo Spectronic, Cambridge, UK). Dull and bright spectra refer to the filters used in experiment 1 and UV/bright ± to those used in experiment 2. UV ± (F) are the spectra of the filters used throughout the fluorescence experiments in part 2.

colours often look particularly conspicuous to humans). Second, it may be the absorption of UVA via fluorescence that produces a more saturated colour, particularly in contrast to UVA-reflecting plumage patches nearby. Alternatively, the fluorescence may simply be a by-product of this unusual pigment and have no signalling role, despite the fact that it can be observed by humans under intense UVA illumination (from black lamps).

Budgerigars, which are our study species, are sexually dimorphic, monogamous members of the parrot family that occur throughout the arid zones of inland Australia (Juniper & Parr 1998). Like passerines, they have a UV-sensitive cone type in their retina, with peak sensitivity (λ_{max}) at 371 ± 5 nm (Bowmaker *et al*. 1997; Wilkie *et al*. 1998) and are known to have plumage reflecting UV wavelengths (Finger 1995). In addition, budgerigars are one of the species of parrot that exhibit fluorescence from their crown and cheek patches (Volker 1937; Boles 1991). However, to the authors' knowledge, any relationship between fluorescence and mate choice has not been published for any bird or, indeed, any animal species. We address this issue experimentally and, in addition, present the most comprehensive set of experiments linking UV reflectance to hue-based mate choice for any non-passerine, and only the second of their kind for any bird (after Bennett *et al*. 1996).

2. METHODS

(a) *Subjects*

Twenty-four female and 32 male wild-type adult (over 1 year old) budgerigars of approximately the same age were obtained from several breeders and each identified with a numbered orange leg band (A. C. Hughes, Hampton Hill, Middlesex, UK). They were housed indoors in single-sex groups of four in visual but not acoustic isolation from other such groups under a 16:8 L:D photoperiod. Lighting was via Truelite fluorescent tubes (Full Spectrum Lighting Ltd, High Wycombe, UK) in high-frequency ballasts in order to simulate daylight (Bennett *et al*. 1996; Hunt *et al*. 2001). All the birds were supplied with a diet of commercial budgerigar mix and millet, plus lettuce, carrot and abundant water in order to stimulate breeding condition. The females developed the brown cere that is indicative of readiness to breed (Juniper & Parr 1998). Seed, water and grit were available *ad libitum* and they were given weekly water baths. Water and seed were also provided throughout the experiment in all stimulus cages and the central area. During these experiments, each female was given a choice of four males, none of whom she had seen before.

(b) *Apparatus*

The trials were conducted in an apparatus similar to that described in Bennett *et al*. (1996), although all floors and walls were constructed from aluminium (figure 1*a*). The apparatus consisted of a central cross-shaped area into which the test bird was placed and four stimulus cages positioned at the end of each arm of the cross into which the stimulus males were placed. The base of the apparatus was lined with matt black paper. It was open on the upper surface except for 5 mm × 5 mm galvanized wire mesh, thereby allowing even overhead illumination by 12 evenly spaced (at 10 cm intervals) 180 cm 100 W Truelite tubes suspended 60 cm above the apparatus, which were powered by high-frequency ballasts. The wavelengths available for mate choice were manipulated by filters positioned both vertically between the female and the stimulus cages and horizontally above the stimulus cages (figure 1*b*). In order to mask any preferences based on vocalizations and to reduce any isolation stress, recordings of the sounds emanating from the home cages of the experimental birds were played through four speakers suspended above each arm of the apparatus. Overhead video recordings allowed quantification of the total time spent by the female in each arm of the apparatus.

(c) *Part 1: does UV reflectance play a role?*

Two experiments were conducted in order to determine whether UV reflectance is used in mate-choice decisions. Experiment 1 investigated whether there are any female preferences for assessing males under UV-positive conditions and whether any effects of removing UV on female choice are due to a changed spectral composition (which is related to hue) or a reduction in the overall quantal flux (which is related to brightness). Experiment 1 also tested whether females have preferences for particular lighting conditions in the absence of males. Experiment 2 investigated whether manipulation of UV reflectance affects social

preferences for same-sex individuals and sought to verify that the apparatus measures heterosexual preferences.

(i) *Experiment 1*

There were four treatments and 16 trials, with the treatments allocated to positions in the test apparatus using Latin squares. The treatments involved four different filter types positioned vertically between the arms and the stimulus cages (figure 1*a*,*b*). These formed a 2×2 factorial design testing for the effects of the overall quantal flux (brighter versus duller) as well as spectral composition (UV-positive versus UV-negative).

Each trial consisted of three consecutive 2 h phases. The first and last were control phases where only the female was present, while the second was a mate assessment phase which included the stimulus males. The former were conducted in order to test for light environment preferences that are unrelated to mate choice (Bennett *et al*. 1996).

(ii) *Experiment 2*

A 2×2 design was again used here: UV-positive versus UV-negative (figure 1*b*) and male versus female conspecifics as stimuli, resulting in four treatments and eight 2 h trials, which were allocated using two Latin squares. Empty cage control phases were considered unnecessary, as they had been used in experiment 1.

(d) *Part 2: does fluorescence play a role?*

This series of experiments was conducted in order to determine whether fluorescence plays a role in mate-choice decisions and whether there is any interaction between fluorescence (through UV absorption) and UV reflection from different plumage regions.

(i) *Experiment 3*

Sixteen females and 32 males were randomly assigned to 16 trials in a balanced way, with one female in the centre of the apparatus and a male in each of the four stimulus cages. Each male was used in two trials, but a given female never saw the same male twice. In addition to the bank of Truelites in the previous experiments, a 60 cm 20 W UV black light (UVP, Cambridge, UK) was fitted 30 cm above each stimulus cage and powered by high-frequency ballasts (Fitzgerald Lighting, Bodmin, Cornwall, UK). These black light tubes have an emission peak at 365 nm, while the majority of visible light is filtered out. As such, the UV component of the irradiance was enhanced relative to the Truelite-only illuminant of part 1. Each trial involved two consecutive 2 h phases. The first was a female-only control, as in experiment 1 and the second a mate assessment phase with males present.

Combinations of filters (figure 1*b*) mounted vertically and horizontally resulted in four conditions: UV-positive/fluorescence-positive, UV-positive/fluorescence-negative, UV-negative/fluorescence-positive and UV-negative/fluorescence-negative, which were formed by the 2×2 combinations of the factors UV reflectance (UV) and fluorescence (F). A UV-blocking or UV-transmitting filter was positioned vertically between each arm and its corresponding stimulus cage for the UV-positive/UV-negative manipulation, as in part 1. Equivalent UV-positive and UV-negative filters were fitted horizontally on top of each stimulus cage in order to create the fluorescence-positive/fluorescence-negative manipulation (figure 1*a*). Thus, an overhead UV-negative filter blocked UV from the illuminating light for the fluorescence-negative condition, hence preventing the excitation of any fluorescent pigments in the plumage of the stimulus male beneath. In contrast, overhead UV-positive filters transmitted UV wavelengths from the illuminant in fluorescence-positive conditions, hence allowing fluorescence. The design thus allowed us to test for an effect of fluorescence independent of UV reflectance (i.e. by comparing the UV-positive/fluorescence-positive and UV-negative/fluorescence-negative treatments). A corresponding test for the effect of UV reflectance in the absence of fluorescence is not really possible as the horizontal fluorescence-negative filter used in the UV-positive/fluorescence-negative and UV-negative/fluorescence-negative treatments blocks most UV from the illuminant, thus removing most of the UV reflectance in both conditions as well as all fluorescence. Removing UV from the overhead illuminant abolishes fluorescence, but must also affect the UV reflectance of the neighbouring feathers. Painstaking application of sunblock (as in Andersson & Amundsen (1997) to UV-reflecting areas) to the fluorescent but not the UV-reflecting feathers might produce a truly UV-positive/fluorescence-negative treatment; however, the plumage patterns were too fine-grained for this to be feasible. Furthermore, we expect preening, rubbing and scratching to move the sunblock onto adjacent non-fluorescent but UV-reflecting plumage areas, thereby confounding a simple UV reflectance effect with a fluorescent effect.

(ii) *Experiment 4*

This was a control study that was designed for investigating whether the male display rate changed with treatment and, therefore, potentially affected female choice in the previous experiment. The experiment consisted of eight 2 h trials, with the apparatus set up as in experiment 3. However, this time there was a male in each stimulus cage and a female in every arm of the apparatus, with the females blocked into each arm with barriers (figure 1*a*). The data collected were the total time that the male spent in a preset 'display area', namely a 10 cm deep, rectangular space running parallel to the filter. It was in this area that the males performed the majority of their display behaviours, such as head bobbing. The resolution of the video images was insufficient for accurate quantification of the frequency of specific behaviours, although it was evident that the males were displaying to the females.

3. RESULTS

(a) *Part 1: does UV reflectance play a role?*

(i) *Experiment 1*

This analysis was by balanced ANOVA, with trial as a random effect and brightness (bright or dull), UV (positive or negative) and phase (control 1, mate assessment or control 2) as three fixed effects. The data from one trial had to be abandoned due to a faulty set-up. In order to normalize the residuals, time as a proportion of trial length was arcsine square-root transformed. There was an overall effect of UV ($F_{1,14} = 9.33$ and $p = 0.009$) and a brightness × phase interaction ($F_{2,28} = 3.50$ and $p = 0.044$), so the phases were analysed separately.

There were no significant effects in the first control phase (all $p > 0.5$). However, females spent a significantly greater amount of time in front of the UV-positive males as compared with the UV-negative males in the mate assessment phase ($F_{1,14} = 4.98$ and $p = 0.042$). Brightness had no effect on their choices ($F_{1,14} = 1.07$ and $p = 0.319$) with no significant interactions ($p > 0.4$). Females spent a significantly greater amount of time in front of the least

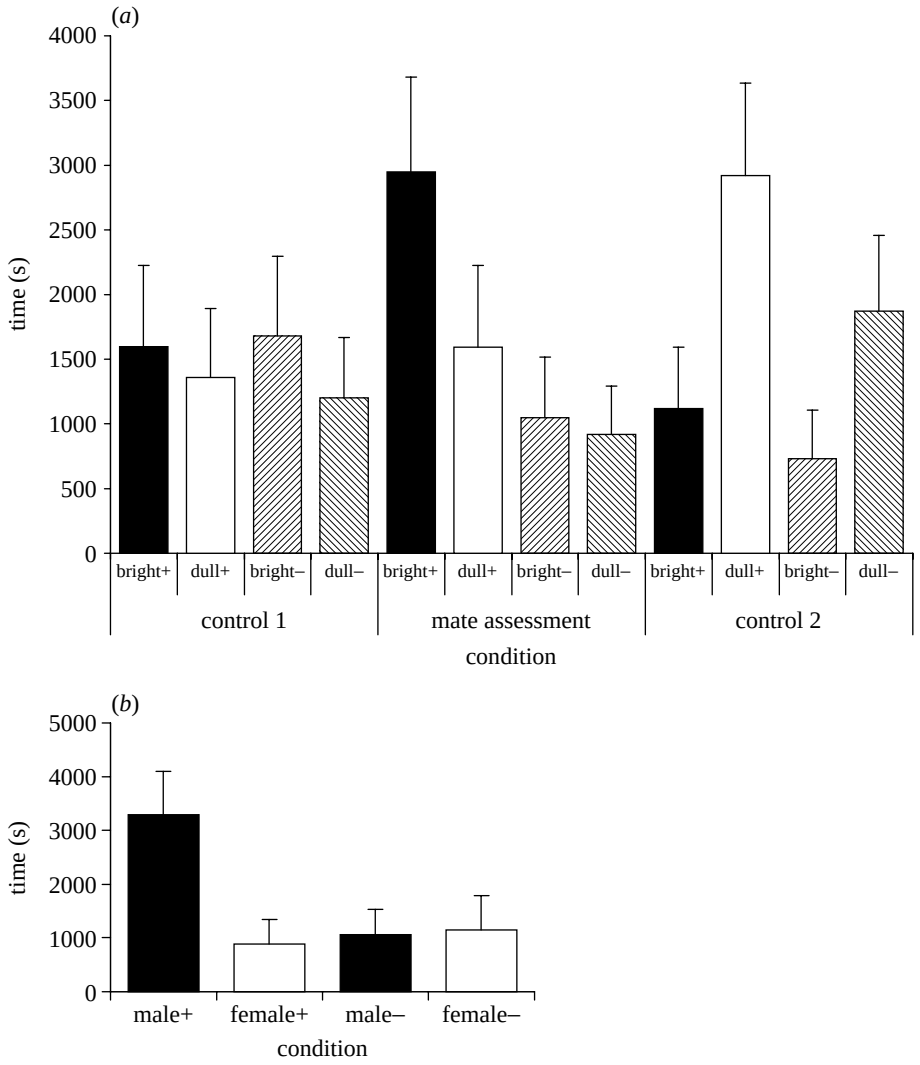

Figure 2. Does UV reflectance play a role? (*a*) The effect of UV reflectance and brightness on the time (+s.e.) that the females spent facing particular males/cages over three phases in experiment 1. (*b*) The effect of UV and sex on the time (+s.e.) that the females spent facing particular stimulus birds in experiment 2.

bright (ND5) stimulus cages as compared with the brightest (ND2) cages in the second control phase ($F_{1,14} = 6.56$ and $p = 0.023$). There were no other significant effects (all $p > 0.2$) (figure 2*a*).

(ii) *Experiment 2*

Again, trial was a random effect, with sex of the stimulus bird (male or female) and UV (positive or negative) as two fixed effects. Overall, females spent a significantly greater amount of time in front of males than females ($F_{1,15} = 6.06$ and $p = 0.025$). There was also a UV × sex interaction ($F_{1,15} = 7.32$ and $p = 0.016$), so the sexes were analysed separately. With respect to males as stimuli, females spent a significantly greater amount of time in front of UV-positive males than UV-negative ones ($F_{1,15} = 8.23$ and $p = 0.012$). There was no effect of UV presence/absence on the amount of time females spent in front of female stimuli ($F_{1,15} = 0.17$ and $p = 0.686$) (figure 2*b*).

(b) *Part 2: does fluorescence play a role?*

(i) *Experiment 3*

This analysis was again by balanced ANOVA, with trial as the random effect and phase (control or mate assessment), fluorescence (presence or absence) and UV (positive or negative) as the three fixed effects. The data were rank transformed prior to the analysis in order to normalize the residuals. Alternative transformations, which preserve the interval scale of measurement, were less effective in normalizing the residuals, but produced equivalent patterns of significant effects. We are therefore confident that the effects detected are robust.

There was a significant three-way interaction between the fixed effects ($F_{1,15} = 5.55$ and $p = 0.033$), so each phase was analysed separately. There was a highly significant UV reflectance × fluorescence interaction in the mate assessment phase ($F_{1,15} = 11.47$ and $p = 0.004$), so the effect of fluorescence was analysed separately for UV-positive and UV-negative conditions. There was no significant effect of fluorescence on the time spent in front of each male in UV-negative conditions ($F_{1,15} = 3.14$ and $p = 0.097$), although there was a trend for a preference of non-fluorescent over fluorescent males. However, the females spent a significantly greater amount of time in front of fluorescent males as compared with non-fluorescent males in UV-positive conditions ($F_{1,15} = 6.09$ and $p = 0.026$). There were no treatment

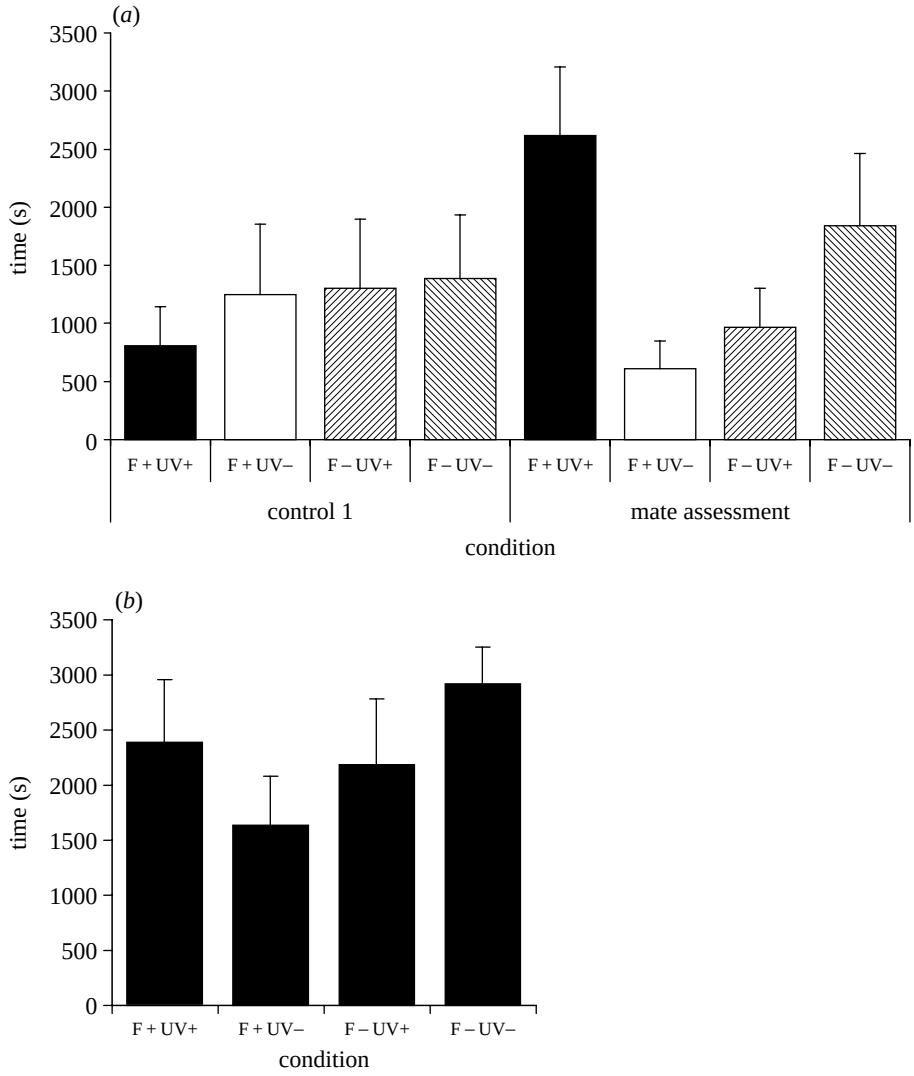

Figure 3. Does fluorescence play a role? (*a*) The effect of the factors UV reflectance and fluorescence on the time (+s.e.) that the females spent facing particular males/cages over two phases in experiment 3. (*b*) The effect of UV and fluorescence on the male display rate, i.e. the time (+s.e.) that each male spent in a preset display area in front of a choosing female in experiment 4.

differences in the female-only control phase, with all $p > 0.5$ (figure 3*a*).

(ii) *Experiment 4*

There were no significant effects of UV or fluorescence on the amount of time the male spent in particular display areas on the floor of the stimulus cages or any interactions, with all $p > 0.3$ (figure 3*b*).

4. DISCUSSION

The results from the first series of experiments provide strong support for the hypothesis that the UVA waveband, to which humans are blind, is used in budgerigar mate-choice decisions. Our results suggest that UV reflectance is an important component of plumage hue rather than simply enhancing achromatic brightness, and that its important role in sexual signalling does not extend to same-sex preferences. Along with the zebra finch (Bennett *et al*. 1996), to the authors' knowledge this is the most comprehensive set of experiments on UV-based mate choice in any bird. Unlike the zebra finch, the budgerigar also exhibits yellow fluorescence due to the absorption of UV. As UV in the illuminant produces fluorescence from some plumage areas and reflectance from others, these joint effects of UV are likely to be confounded under natural illumination. However, by using filters for manipulating fluorescence in the absence of UV reflectance, our experiments show that fluorescence *per se* (re-emission of longer wavelengths through UVA absorption) does not seem to act as a signal. If fluorescent plumage has a signalling role, it may be through absorbing UV, perhaps thereby enhancing contrast with the UV reflectance of other plumage regions nearby. Before discussing this more speculative role of UVA-absorbing plumage, we first deal with the definite effects of UV reflectance on male attractiveness.

The females in experiment 1 showed significant preferences for viewing males under UV-positive conditions. Although we cannot discount the possibility that this preference extends to light environments in the absence of males (there was no UV × phase interaction), there was no positive evidence for this. Unlike the effect of UV in the mate assessment phase, there was no effect of UV in the control phases when they were analysed separately. Furthermore, the results of experiments 2 and 3 (see

below) demonstrate that the effect of removing UV is most pronounced in heterosexual mate choice.

As there were no differences between the two varying brightness conditions during the mate assessment phase, we can conclude that the preference for UV-positive males is not simply a preference for higher brightness, but that it is because UV reflectance is necessary for correct hue perception. The finding that females spent significantly more time in front of the least bright stimulus cages in the second control phase but not the first was slightly surprising ($p = 0.023$). This may be a result of the general apparatus environment being bright and, thus, once the apparatus is familiar, the females prefer to move to the least bright areas when there are no salient objects to view. The females in experiment 2 consistently preferred males to females, thereby verifying the proposition that our apparatus measures heterosexual preferences in budgerigars and not simply a tendency to flock with conspecifics regardless of sex. We note that this assumption is rarely tested in 'mate choice' experiments (see Bennett *et al*. 1996). As in experiment 1, we found that females preferred UV-reflecting males to non-reflecting males, but also found that no such trend was apparent in same-sex preferences.

By combining the findings from experiments 1 and 2, we can conclude that plumage colours with a UV-dependent component are used in budgerigar mate-choice decisions. This supports previous research that has shown that UV reflections from avian plumage are used in intersexual signalling by conspecifics (reviewed by Cuthill *et al*. 2000*a*). These results also provide support for the proposition that plumage does not need to reflect purely in the UV waveband for UV to be used in mate-choice decisions (Bennett *et al*. 1994, 1997; Cuthill *et al*. 2000*a*). Given that many parrots have UV-reflecting green, yellow and blue plumage (A. T. D. Bennett, I. C. Cuthill, S. M. Pearn, D. C. Paton and E. R. Potapov, unpublished data), it will be interesting to see whether the results we report hold true generally across parrots.

The results from part 2 suggest that the importance of UV in budgerigar mate choice is largely due to UV plumage reflectance rather than fluorescence, as when UV is absent from the illuminant fluorescent males are no more attractive than non-fluorescent males (experiment 3) (figure 3). If females had shown a preference for UV-negative/fluorescence-positive over UV-negative/fluorescence-negative males, our design would have provided clear evidence of a fluorescence effect. By using black lights for enhancing the UV irradiance in part 2, we biased the experiment in favour of finding a fluorescence effect on attractiveness, yet did not find one. Thus, we feel confident that, if fluorescent plumage has a signalling role in nature, where the proportion of UV in the illuminant will be much lower (and more similar to that used in part 1), it is not through any enhanced long-wave (yellow) hue. So, how do we explain the significant preference for UV-positive/fluorescence-positive over UV-positive/fluorescence-negative males in experiment 3 if it is not due to fluorescence via UVA-induced long wavelength emissions?

It should be noted that, in part 2, the UV-positive/fluorescence-positive condition gives rise to an increased intensity of UV reflectance from the stimulus males when compared with the UV-positive/fluorescence-negative condition. This is because the extra UV wavelengths from the black light are being transmitted through the horizontal UV-transmitting filter thereby leading to both an increased intensity of UV reflection and an increased intensity of UVA-induced fluorescence. However, it seems unlikely that it is higher achromatic brightness that the females prefer under these conditions. This is because, in experiment 1, a direct test for achromatic brightness effects that resulted in increases in the quantal flux from 300–700 nm did not show any effect on the environment in which the female preferentially viewed males ($p = 0.319$). Furthermore, the non-significant preference for UV-negative/fluorescence-negative over UV-positive/fluorescence-negative males in experiment 3 is in the opposite direction to that predicted for an achromatic brightness effect.

Whilst achromatic brightness may not be important, budgerigars have various colours with a UV-reflecting component, including violet, UV green and UV yellow. Under UV-positive/fluorescence-positive compared with UV-positive/fluorescence-negative conditions, these colours will be more highly saturated. These changes in saturation may be what affected female choice in experiment 3.

The above explanations refer to single plumage regions, but contrast with adjacent or nearby plumage regions may also be important. Fluorescent regions occur next to highly UV-reflective regions in the budgerigar, such as their violet cheek patches. Fluorescent plumage may increase the contrast with these nearby patches. In this way, fluorescent plumage may have a signalling role, but it is not the enhanced long-wave radiance of fluorescence that is important so much as the fact that the plumage absorbs UV. Consequently, in experiment 3, the lack of a preference for UV-negative/fluorescence-positive over UV-negative/fluorescence-negative males could be due to an absence of UV reflection and, thus, lack of contrast between nearby regions. However, further experiments will be required in order to test this hypothesis.

Overall, the four experiments reported here clearly show that UV wavelengths play a role in budgerigar mate-choice decisions and that this is most probably via alteration of female choice due to changed reflectance of the male in the UVA waveband. Experiment 4 revealed that the male display rate did not vary with light treatment. The assumption that the stimulus (as opposed to the test) animals are unaffected by the treatment is rarely tested in mate-choice experiments. Consequently, we have added evidence that the effects we observed in both parts 1 and 2 are due to the altered visual appearance of males affecting female choice rather than some change in male activity being causal. However, as preferences were not shown under UV-negative conditions in experiment 3, the long wavelength re-emission aspect of fluorescence does not seem to be the key signal element. The fact that some parrot plumage appears particularly conspicuous to humans and can be made to fluoresce need not mean that it is the enhanced long-wave radiance that affects sexual signalling.

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Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*

Sophie M. Pearn, Andrew T. D. Bennett and Innes C. Cuthill

On page 2275, § 2d(i), the word 'negative' was incorrectly printed as 'positive'. The 13th sentence of this sub-section should read:

The design thus allowed us to test for an effect of fluorescence independent of UV reflectance (i.e. by comparing the UV-negative/fluorescence-positive and UV-negative/fluorescence-negative treatments).