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Plumage maintenance affects ultraviolet colour and female preference in the budgerigar

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ABSTRACT

Elaborate or colourful feathers are important traits in female–mate choice in birds but little attention has been given to the potential costs of maintaining these traits in good condition via preening behaviour. While preening is known to be an important component of plumage maintenance, it has received little attention with respect to colouration. We investigated whether preening can influence plumage reflectance and whether females show a preference for plumage cleanliness in captive-bred, wild-type budgerigars, *Melopsittacus undulatus*. To do this, we compared the spectral colour of birds that were allowed to preen their plumage and individuals that were prevented from preening. The plumage of birds that were prevented from preening showed a significant lower reflectance in the UV range (300–400 nm). Subsequently, we measured females' preferences for preened and unpreened males using a two-choice test. In a second experiment we allowed females to choose between an unpreened male and a male smeared with UV-absorbing chemicals (UV-blocked male). The proportion of time that females stayed near preened males was statistically higher than for unpreened males, but females spent similar amounts of time with unpreened males and UV-blocked males. These results are consistent with the idea that female budgerigars are able to discriminate between preened and unpreened males, and that UV colours, mediated by preening, can convey information about a bird's current condition.

1. Introduction

Females use various signals to assess the quality of males, including vocalisations, behavioural displays, pheromones and morphological traits (Andersson, 1994). Honest advertisement theory suggests for signals to contain reliable information on mate quality that they must be costly to produce and/or to maintain ('handicap costs', Zahavi, 1975; Grafen, 1990). Production costs of morphological traits are usually restricted to a limited time period during which the trait is developed. Apart from any negative impact on fitness that a handicap trait may have (e.g. elongated tail feathers may increase the risk of predation), costs may also arise from keeping ornamental traits in order (e.g. Walther and Clayton, 2005; Griggio and Hoi, 2006). In birds, plumage ornamentation is one of the most common traits involved in mate choice (Hill and McGraw, 2006). In particular, brightly coloured feathers have been repeatedly found to indicate quality and condition of birds at time of moult (e.g. Lozano, 1994; McGraw and Hill, 2000; Blount et al., 2003; Serra et al., 2007). However, feather colours can, and do, change after moult because of bacterial degradation (Grande et al., 2004), the addition of preen waxes (e.g. Surmacki and Nowakowski, 2007), mechanical abrasion (Willoughby et al., 2002), exposure to sunlight (Surmacki, 2008) or dirt accumulation (Zampiga et al., 2004).

Birds spend time and energy maintaining their feathers in good condition and ornamented species, with longer plumage than non-ornamental species, devoted significantly more time to preening (Walther and Clayton, 2005). Removing the soiling and dirt from their feathers or controlling ectoparasites (Cotgreave and Clayton, 1994; Walther and Clayton, 2005) results in a temporal trade-off between investment in plumage maintenance and other activities, such as foraging and vigilance (Redpath, 1988; Cucco and Malacarne, 1997). Despite the important role of preening in the maintenance of plumage colours and, hence, in mediating male mating success, few recent studies have addressed this point (Zampiga et al., 2004; Montgomerie, 2006; Lenouvel et al., 2009; Roberts et al., 2009). Unfortunately, these studies each employed different methodological approaches and, not surprisingly, obtained contrasting results. For example, one study (Montgomerie, 2006) assessed the effect of dirt accumulation on the feathers of three bird species using museum specimens (house sparrow, *Passer domesticus*: white breast/belly feathers; pine grosbeak, *Pinicola enucleator*: red breast plumage; evening grosbeak, *Coccothrauses vespertinus*: yellow breast plumage). Comparing the

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reflectance spectra of washed and unwashed feathers he found that the accumulation of dirt on the feathers causes a reduction of reflectance which is more pronounced in the human-visible part of the reflectance spectra than in the shorter, ultraviolet wavelengths that birds can also see. Lenouvel et al. (2009) soiled with wheat flour the yellow feathers (carotenoid-based colouration) of male canaries, *Serinus canaria*. The effect of soiling was to increase the brightness of the plumage (presumably because of the wheat flour used for soiling), and it seems unlikely that in natural conditions unpreened/soiled birds have brighter colours that clean birds. Thus, while this study highlights the importance of preening in maintaining plumage colour, it says little on the effect of soiling in more natural conditions. In a third study, Zampiga et al. (2004) artificially soiled (with dust and a water-sugar solution on the breast) a group of blue-type budgerigars, *Melopsittacus undulatus*, and compared the reflectance spectra of birds that were subsequently allowed to preen with those of birds that were prevented from preening. Their results demonstrated that soiled birds that were prevented from preening showed a reduced reflectance in the shorter bird-visible wavelengths (<420 nm) and were least preferred in a mate choice test where females could choose between a preened and an unpreened male. These results are consistent with indirect evidence from field studies (Örnborg et al., 2002; Delhey et al., 2006). This is probably because soil particles on the feather surface optically interfere with the light as it emerges from the nanoscale structures into the barbules, responsible of the production of structural colours (Prum, 2006).

Whether or not soiling (and hence preening) differentially affects structural colours remains to be clarified, and has important implications for our understanding of the evolution of this type of colour. It is well established that a large number of bird species are capable of detecting wavelengths in the UVA portion of the spectrum (320–400 nm; Cuthill, 2006) and UV-reflective plumage is common in many avian taxa (e.g. Mullen and Pohland, 2008). Moreover, several behavioural studies have demonstrated that UV colours are important signals in mate choice and can also function as signals of social status or for parent-offspring communication (Bennett et al., 1996; Andersson and Amundsen, 1997; Hill and McGraw, 2006; Korsten et al., 2006; Tanner and Richner, 2008). Assuming that individuals in poor condition invest less in maintenance, one would predict that preening behaviour is directly mirrored in plumage reflectance. It has, therefore, been suggested that plumage colouration (in particular in the UV range) may be a very sensitive and reliable indicator of the current health status of an individual (Zampiga et al., 2004). Anyway, a study with a natural way of soiling is necessary to investigate this hypothesis. Another limitation of the previous study was to test mate preference for UV colouration by presenting females with males behind UV-blocking filters, indeed the entire environment behind the filter is modified (see also Hill and McGraw, 2006).

We first examined how plumage reflectance of naturally soiled, unpreened, breast feathers compares to that of preened feathers in wild-type (green) budgerigars. In this species the green breast colouration is a combined colour containing both a yellow pigment component and a blue structural component. Second, we investigated whether there is a female preference for preened males. To achieve this, we compared the spectral colour of birds that were normally able to preen their plumage and individuals that were prevented from preening. Subsequently, we measured female preference for preened and unpreened males using a two-choice test. In a second experiment we allowed females to choose between an unpreened male and a male smeared with UV-absorbing chemicals (UV-blocked male). We predicted that UV reflectance would be affected by dirt accumulation on the feathers, and that preened males would be preferred by females.

2. Methods

2.1. Study species, soil, colour manipulation and reflectance measurements

Colour measurements were taken on the throat-breast green feathers from male wild-type budgerigars of approximately the same age (over 1-year old), obtained from several breeders. During winter–spring 2005 and 2007, 120 male budgerigars were selected haphazardly from four outdoor aviaries where females were present (Griggio et al., 2010). No individuals were moulting during this study. Males were divided into two groups, one with neck collars (unpreened group, $n = 60$) and one without neck collars (preened group, $n = 60$). Before the experiments started standard measurements of wing length and body mass for all males were taken. All birds from both groups were placed in individual indoor cages (50 cm × 50 cm × 50 cm), and water and food were provided ad libitum before and during the experiments. The soft plastic collar prevented preening but allowed the birds to carry out their normal activities (authors' pers. obs. and Zampiga et al., 2004). Moreover, preliminary observations of individually caged males confirmed that plastic collars did not affect the body mass of these individuals. Males were individually caged for about 36 h in cages dirtied with a mixture of avian preen gland fat (*oil du canard*, referred as ODC), sand, and fruit pulp (kiwis and oranges), distributed on the cage floor, on the perches, and on the margins of the water and food dispensers. Before the female choice test commenced were randomly chosen from the preened group 30 males (UV-blocked males) to whom was applied a mixture of UV-blocking chemicals (Parsol 1989 and MCX, Roche, Switzerland) and ODC (Andersson and Amundsen, 1997; Sheldon et al., 1999; Korsten et al., 2006). On the rest of the males (preened and unpreened males), were smeared only the ODC. Plumage reflectance was measured before the beginning of the experiment and after 1 day when the female choice test commenced.

Reflectance in the 300–700 nm range was measured with an Ocean Optics, Inc. USB 2000 spectrometer and a deuterium-halogen light source (DH-2000). Reflectance spectra were measured at 45° of light incidence (illumination and reflectance at 45° to the sample's surface). A software package (Spectrawin 4.2) computed reflectance spectra relative to a white reference tile (SW-2). For each individual male, five spectral measurements (each spectrum averaged from five scans) were taken from throat-breast feathers and the probe removed between each measurement. Then the five measurements were averaged for each male before and after manipulation. The colour was quantified using standard tristimulus descriptors of reflectance spectra: brightness, chroma and hue (Griggio et al., 2010). Mean brightness was calculated as the mean reflectance ($R_{300–700\,nm}$). UV chroma was calculated as the sum of reflectance in the UV part of the spectrum divided by the sum of total reflectance ($R_{300–400\,nm}/R_{300–700\,nm}$). Hue ($\lambda_{Rmax}$) was calculated as the wavelength at peak reflectance. These indices have been used in previous studies on birds (Hunt et al., 1999; Sheldon et al., 1999; Griffith et al., 2003; Liu et al., 2007; Griggio et al., 2009).

2.2. Female preference: Experiment I and Experiment II

Details of female preference experiments can be found in Griggio and Hoi (2006). Here are summarised critical components of the experiments. Sixty stimulus males were randomly allocated to the unpreened and preened group (see above). Female–mate choice trials were conducted in a two-choice indoor chamber (2 m × 0.5 m × 0.5 m). All the females used in the three experiments (see below) developed the brown cere, signalling their readiness to breed (Juniper and Parr, 1998). Females were placed in the central chamber where they were allowed to choose between two simul-