Plumage maintenance affects ultraviolet colour and female preference in the budgerigar

Matteo Griggio [a,*], Herbert Hoi [a], Andrea Pilastro [b]

[a] Konrad Lorenz Institute for Ethology, Savoyenstrasse 1/A, A-1160 Vienna, Austria
[b] Dipartimento di Biologia, Università di Padova, Via U. Bassi 58/B, I-35131 Padova, Italy

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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.

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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

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-

Table 1
Wing length and body mass before and after the treatment (using dirty cages) of male budgerigars used in the two mate choice experiments: ±SE are shown.

Variable	Experiment I		F	P	Experiment II		F	P
	Unpreened (n = 30)	Preened (n = 30)			Unpreened (n = 30)	UV-blocked (n = 30)		
Wing chord (cm)	10.88 ± 0.07	10.81 ± 0.08	0.37	0.54	10.92 ± 0.18	10.67 ± 0.07	1.64	0.20
Body mass before (g)	42.92 ± 0.99	44.33 ± 0.93	1.08	0.30	45.10 ± 1.19	43.75 ± 1.06	0.72	0.40
Body mass after (g)	42.32 ± 1.05	43.78 ± 1.02	0.99	0.32	45.12 ± 1.20	43.60 ± 1.06	0.95	0.35

taneously presented males in one of the compartments on each side. Three opaque partial dividers were erected to reduce the possibility that females might simultaneously observe both males (no choice area) and that the two males might interact. A nest box was provided in the middle of the central chamber in order to stimulate breeding conditions. Water and food were provided to all birds before and during the experiments. The experimental aviary was illuminated by artificial and natural light (the ambient light in the experimental room contained UV wavelengths) through windows (under 14:10 L:D photoperiod). To better acclimatize individuals, calls from the aviaries were recorded and played back during the experiments (Pearn et al., 2001; Griggio and Hoi, 2006) from a speaker situated in the centre of the experimental room (at the same distance from the two stimulus chambers). Treatment and control males were alternated with respect to the side of the central cage. Behavioural observations were made from a hide 3.5 m away. In the late afternoon before the stimulus males were presented to females, males were placed in the two side compartments and allowed to acclimate. At this point the neck collar was also applied to the preened birds and the old neck collar was replaced with a new one for the unpreened birds, so both males were wearing a neck collar during the choice test. The experimental observations were carried out between 07.00 a.m. and 11.00 a.m. local times. The female was introduced into the apparatus in the morning (about 2 h before the trial commenced); two opaque partitions were erected between the female and males to prevent visual contact. Twenty minutes after the manipulation, the opaque partitions between the female and males were replaced by a wire mesh metallic net and we recorded the position of the female every 15 s for 30 min. It was measured the time females spent on each side (left area, no choice area, right area) of the mate choice arena, and bias for right or left side (in front of a particular male) was regarded as mate preference.

In the second experiment (Experiment II) was used the experimental design of Experiment I but instead compared unpreened to UV-blocked males. In the two experiments was used a different female for every dyad of males.

2.3. Statistical analyses

The effects of the experimental manipulation for each colour parameter and body mass through time (before and after the manipulation) were evaluated using repeated-measures ANOVA. Statistical analyses were performed using SPSS v. 13.0 (Norušis, 1993). Data were checked for normality, and appropriate transformations were used when necessary. Throughout the paper statistical tests are two-tailed and p-values less than 0.05 are considered significant. All the results are presented as mean ± SE.

3. Results

3.1. Soil and colour manipulation

In both experiments there was no significant difference between these two groups of males for body mass (±0.1 g) and wing length (±0.1 mm) (Table 1). The treatments effectively changed the plumage reflectance of male budgerigars (Figs. 1 and 2). Soiling decreased plumage reflectance in the
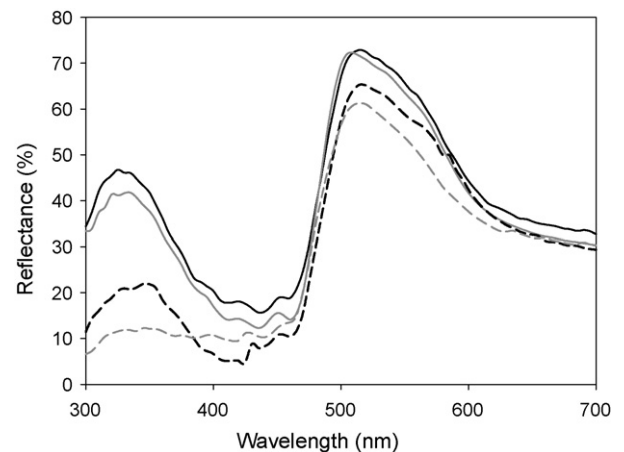

Fig. 1. Average reflectance spectra from breast feathers of 120 wild-type male budgerigars, before and after the treatment in which they were kept in dirty cages. Black solid line represents males before treatment (n = 120); grey solid line represents males after treatment that have been allowed to preen (n = 30); black dashed line represents males after treatment that have been prevented from preening (n = 60); grey dashed line represents males after treatment and with the application of UV-blocking chemicals (n = 30). Illumination and reflectance at 45° to the sample's surface.

males that were prevented from preening, while the males that could preen had only a minor decrement in their plumage reflectance (Figs. 1 and 2). There was not a significant effect of time and treatment on hue (time: $F_{1,117} = 1.2$, $P = 0.28$, treatment: $F_{2,117} = 2.35$, $P = 0.10$, time × treatment: $F_{2,117} = 0.50$, $P = 0.61$; Fig. 2A). Both time and treatment significantly influenced brightness, but no time × treatment interaction was significant (time: $F_{1,117} = 55.07$, $P < 0.001$, treatment: $F_{2,117} = 9.99$, $P < 0.001$, time × treatment: $F_{2,117} = 0.48$, $P = 0.62$; Fig. 2B). There was a statistically significant effect of time and treatment on UV-chroma (time: $F_{1,117} = 61.64$, $P < 0.001$, treatment: $F_{2,117} = 8.71$, $P < 0.001$, interaction: $F_{2,117} = 6.97$, $P = 0.001$; Fig. 2C). Therefore our treatment was successful in manipulating the UV intensity, allowing us to consider how dirtiness and UV reduction might affect female preferences. Body mass of males during the experiment did not decrease significant (time: $F_{1,117} = 2.18$, $P = 0.14$, time × treatment: $F_{2,117} = 0.24$, $P = 0.79$; see also Table 1).

3.2. Female preference

Budgerigar females showed preferences for clean males (preened) in the two-choice test (Experiment I) where preened and unpreened (less UV) males were used as stimulus (paired t-test: $t_{29} = -3.47$, $P = 0.002$), but these preferences disappeared when we used males with UV-blocking chemical products (UV-blocked males) instead of preened males (Experiment II: paired t-test: $t_{29} = 1.38$, $P = 0.18$, Fig. 3). Lastly, there were no significant differences in female preferences based on other male plumage colorimetrics or male body size (hue, brightness, body mass and wing length were used as a covariate in GLM analyses, data not shown).
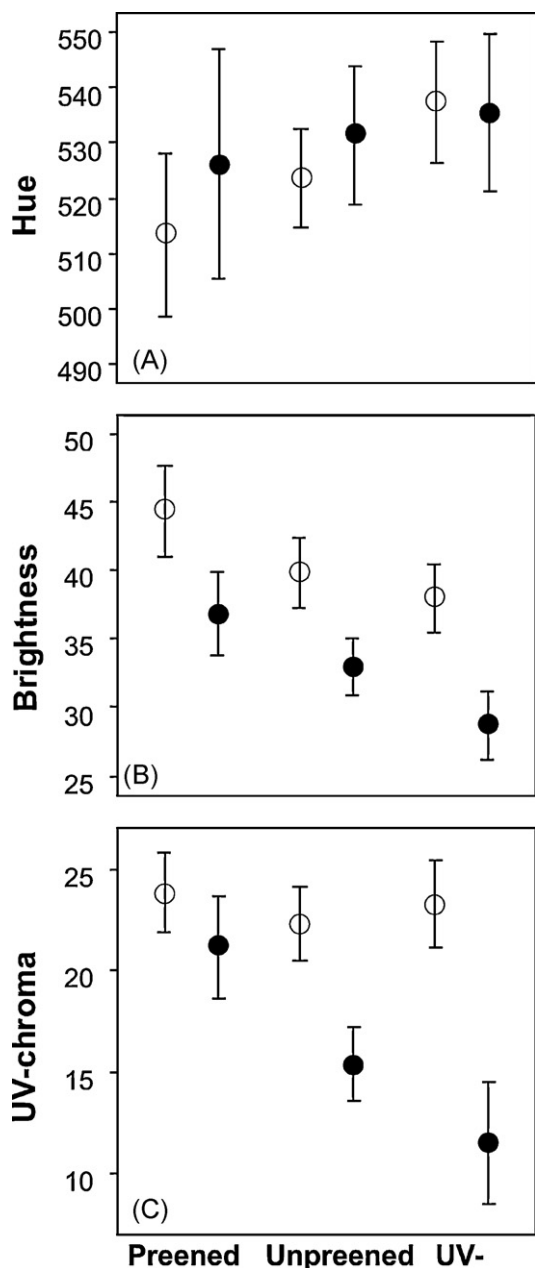
Fig. 2. Means and ±SE of the hue (A), brightness (B) and UV-chroma (C) for the three groups of stimulus males (preened, $n = 30$; unpreened, $n = 60$; and males with UV-blocking chemicals, $n = 30$), before (white circles) and after (black circles) the treatment.

4. Discussion

Our experimental treatment effectively changed the plumage colouration of male budgerigars. In particular, when preening was impaired the plumage reflectance was reduced along the entire spectrum, but particularly in the UV range. This indicates a key role of preening in maintaining feather colours and, in particular, of UV reflectance. This result suggests that structural colours are sensitive to plumage maintenance and may signal male condition after feathers have grown. When budgerigar females were given a choice between a preened and an unpreened male they showed a significant preference for preened males. The results of the first experiment suggest that female budgerigars discriminate between preened and unpreened males and prefer clean, preened, males. Females, however, did not discriminate between unpreened males
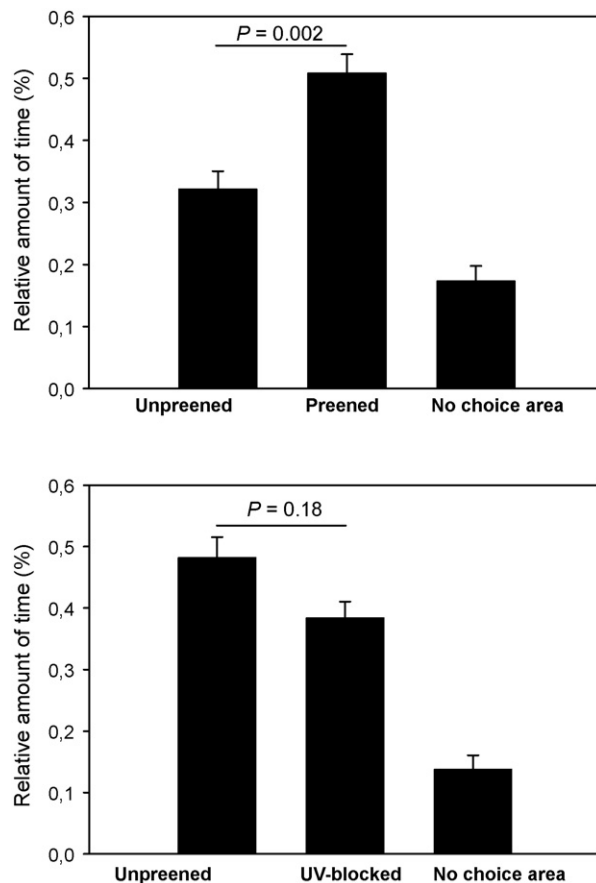
Fig. 3. Results of the female–mate choice experiments, showing the mean relative time (±SE) spent by females near (top) unpreened males ($n = 30$), preened males ($n = 30$) and in the no-choice area (Experiment I); (bottom) unpreened males ($n = 30$), UV-blocked males ($n = 30$) and the no-choice area (Experiment II).

and males whose UV feather reflectance was reduced by applying an UV-blocking chemical. The results of the second experiment suggest that this preference is likely to be due to the reduction of the UV feather reflectance, probably associated with an accumulation of dirt on the feathers, and probably not to plumage disarrangement caused by the absence of preening, as females did not discriminate between unpreened males and UV-blocked males that could normally preen. Additionally, our results confirm that budgerigar females prefer males whose plumage has high UV reflectance (Pearn et al., 2003; Zampiga et al., 2004).

One of the most difficult problems in evolutionary biology is to identify the costs of particular ornaments used in mate choice context, and many hypotheses have been proposed to solve the question: 'Why should individuals have a sexual preference for exaggerated or particular coloured traits?' In birds, structural colouration remains the least studied of the three most important feather colour-producing mechanisms (melanins and carotenoids being the other two; e.g. Senar, 1999; Olson and Owens, 1998; Griggio et al., 2007; Serra et al., 2007). Some studies suggest that the expression of structural colouration is influenced by the nutritional condition of an individual at the time of moult (Keyser and Hill, 1999; Doucet, 2002; but see Prum, 2006), by the intensity of blood parasites infection (Doucet and Montgomerie, 2003), or by the duration of the moult (Griggio et al., 2009). Others suggest that UV colours may signal development stability and, so, the genetic quality of the individual (Fitzpatrick, 1998; Andersson, 1999), but to our knowledge this idea remains untested. Whatever the costs involved in the production of structural colours, here we propose that plumage maintenance represent a potential

cost. In a comparative study Walther and Clayton (2005) found that species with more elaborate plumage ornaments spend more time in maintenance behaviour than non-ornamented species. Therefore, this 'high maintenance' cost could reinforce the honesty of ornamental plumage. Preening may offer a reinforcement to maintain the honesty of a trait that is already expensive to produce, or may be important for the efficacy of feather signals that in turn directly affect male attractiveness (Zampiga et al., 2004). The honesty of the final product is guaranteed by the time devoted to preening behaviour. Birds spend time and energy to maintain ornamental traits in good condition (Cotgreave and Clayton, 1994), and thus results in a temporal trade-off between investment in plumage maintenance and other activities (Redpath, 1988; Cucco and Malacarne, 1997). Studies of sexual selection should therefore take into account variation in the ability of individuals to keep ornaments in good condition (e.g. Barbosa, 1996; Clayton et al., 2005; Walther and Clayton, 2005; Roulin, 2007).

It must be noted that during preening an individual uses oil from the uropygial gland, and that and the ordering of barbs and barbules could affect the UV-reflectance properties of colour feathers (Montgomerie, 2006). The idea that preen wax enhances bird plumage colouration has already been studied and no effect of preen wax on plumage colouration has been detected (Reneerkens and Korsten, 2004). One study found that the presence of soil and preen wax influenced plumage colouration, but the relative contribution of soil and wax in influencing the change in colour (Surmacki and Nowakowski, 2007) was not clear, nor was the effect of dirtiness in the UV range directly studied (see also Piault et al., 2008). However, further studies are necessary to investigate the influence of preen wax on UV-reflectance properties of feathers (Delhey et al., 2008). Moreover, there are no studies, to our knowledge, on the ordering of barbs and barbules and the possible effect on the reflectance properties of colour feathers. Further studies are needed to clarify the role of preening behaviour to maintain barbs and barbules in order and the effects this could have on UV reflectance.

In conclusion, our results conjointly with recent studies (Örnborg et al., 2002; Moyer et al., 2003; Delhey et al., 2006) reveal that plumage colours are a more flexible trait. In particular, maintaining UV-plumage colouration could represent an additional honesty-enforcing mechanism after moult which may be important for female mating decisions. Females may use structural feather colours to extract information about male condition at the time when feathers were grown (Griggio et al., 2009) but also during the subsequent months, as structural feather colours may be particularly sensitive to plumage maintenance.

Acknowledgements

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