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Preening, plumage reflectance and female choice in budgerigars

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Plumage ornaments are important signals in sexual selection context. Plumage maintenance is therefore important not only for insulation and flight but also for ornament efficacy. However, the effect of plumage maintenance on ornament characteristics and female choice has never been investigated experimentally. In this study we focused on the influence of preening on plumage reflectance and, indirectly, on female preference in the budgerigar *Melopsittacus undulatus*. We measured the effect of preening on the reflectance of previously soiled plumage. Our results suggest that soiling affects plumage reflectance in budgerigars that are prevented from preening and that this effect is particularly pronounced in the UV range. In contrast, individuals that were allowed to preen restored their plumage reflectance spectrum to presoiling levels. In a two-choice test, females presented with clean (preened) and soiled (unpreened) males, spent more time near the clean male. These results suggest that female budgerigars are able to discriminate between preened and unpreened males. Further investigations, conducted under various soiling conditions, are necessary to confirm the effect of soiling on plumage reflectance spectrum and to investigate which cues are used by females to discriminate between preened and unpreened males. Such research could reveal whether UV feather ornaments, mediated by preening, are special signals conveying information about a bird's current condition.

KEY WORDS: ultraviolet colours, sexual selection, plumage condition, ornaments, *Melopsittacus undulatus*

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INTRODUCTION

Bird plumage is composed of down and small cover feathers that function mainly to insulate the body from heat loss, and of flight feathers, which form the flight organs, wings and tail. Both functions are vital and thus it is extremely important to maintain the plumage in good condition. Preening is perhaps the most important behaviour in this context (e.g. Walther & Clayton 2004), and it serves the purposes of cleaning, arranging and generally maintaining the plumage by oiling and ordering the feathers and by removing dirt and parasites (Campbell & Lack 1985). Birds usually invest considerable time in preening (Cotgreave & Clayton 1994), which is done as a routine activity, in response to soiling or disarrangement of the feathers, and because of skin irritation (Campbell & Lack 1985: 102).

The function of the plumage, however, is not limited to flight and insulation. In many bird species feathers are coloured and also have the function of producing visual signals, such as distinctive feather patches that serve communication in both social and sexual contexts (e.g. Rowher & Rowher 1978, Veiga & Puerta 1996, Saetre et al. 1997). In particular, several studies have demonstrated that plumage colouration is important in female choice (Andersson 1994). Indeed, males are usually the most colourful sex and several studies have demonstrated that females prefer brightly coloured males (e.g. Johnsen et al. 1998, Hill 1999). Avian feather colours are produced by two main colour mechanisms: pigments, such as carotenoids and melanins (Brush 1978), and structural colours, in which physical structures inside the feathers produce colour by differential scattering of certain wavelengths of light (Dyck 1978, Prum et al. 1998).

Numerous studies have provided experimental evidence that variation in both pigmented and structural colours influences female mate choice (carotenoids: see Hill 1999 for a review; structural colours: e.g. Andersson & Amundsen 1997, Bennett et al. 1997, Johnsen et al. 1998, Pearn et al. 2001, Delhey et al. 2003, but see Perrier et al. 2002). Coloured feathers have been often considered as "static" ornaments, which are formed when the feathers grow and are not changed until the next moult. Evidence that this may not always be the case, however, is starting to be reported (Örnborg et al. 2002, Willoughby et al. 2002, McGraw & Hill 2004). Therefore preening and maintaining the plumage in good condition may also be important in the context of inter-sexual selection. For example, if cleaning (removing dirt and fat) and ordering the plumage affect the reflectance properties of coloured feathers, preening may in turn affect male attractiveness. In line with this argument, male birds invest more time in preening than females (e.g. Møller 1991, Cotgreave & Clayton 1994 — although this may be explained by the fact that during the breeding season males may be less time-constrained than females), and species with more elaborate feather ornaments devote more time to plumage maintenance (Walther & Clayton 2004). Plumage condition is also affected by ectoparasites, such as chewing lice, which may also alter colours, for example by selectively damaging certain feathers or feather parts (e.g. Kose & Møller 1999). In this context, preening may have an additional, indirect beneficial effect on plumage maintenance by reducing the ectoparasite load (Clayton & Moore 1997, Rozsa 1993). Plumage maintenance is therefore likely to be important for the efficacy of feather signals.

Despite the potential importance of preening in removing the dirt and oiling from the feathers, we are not aware of any experimental study on the influence of preening on feather reflectance. In the present study we aimed first at evaluating whether preening affects the reflectance spectrum in budgerigars (*Melopsittacus undulatus*) that were previously artificially soiled. Our second aim was to investigate whether females discriminated between males that could preen their plumage normally after having been artificially soiled and their male counterparts that were prevented from preening. In our analyses we considered the whole wavelength spectrum including the UV, because UV colours seem to be affected by plumage condition (Örnborg et al. 2002) and preening could therefore be important in this colour range. The socially monogamous budgerigar is therefore an ideal species for such an investigation because (i) their plumage reflects in the UV range (Pearn et al. 2001) and their eyes have a cone type with the peak in the UV (Bowmaker et al. 1997, Wilkie et al. 1998); (ii) their plumage properties, in particular UV colours, have a relevant role in mate choice (Pearn et al. 2001).

METHODS

For the experiment, blue-type budgerigars were selected randomly from a captive stock housed in four outdoor aviaries (3 × 5 × 2.5 m). Males and females were kept in separate aviaries preventing visual and auditory contact. Food (a commercial budgerigar mix plus vegetables) and water were provided *ad libitum*. Blue-type budgerigars are not found in the wild (the wild-type is green). However, we used blue-type budgerigars because they present a reflectance spectrum on the breast feather that show high reflectance values in the entire spectrum range perceived by these birds (320-700 nm, see Bowmaker et al. 1997, Wilkie et al. 1998). In contrast, chest feathers of wild-type male budgerigars present two reflectance peaks around 350 nm and 520 nm, as the blue-type birds, but, differently from these latter, have very low reflectance between 400 and 500 nm (see fig. 1a(ii) in Pearn et al. 2003 and Fig. 2 in this study for a comparison). The use of blue-type birds has therefore the advantage of allowing measurement of the effect of soiling and preening on feather reflectance along the entire spectrum visible to budgerigars.

Effect of preening on plumage reflectance

Twelve males were randomly allocated to the preened or unpreened group. The plumage of the males of both groups was artificially dirtied by applying a mixture of sand and soil to the breast feathers on a 3 × 2 cm area of each male. Breast feathers had previously been wetted with honey diluted in water allowing the dust to remain attached to the feathers. A neck collar (a cone of soft, transparent plastic of 6 cm diameter with a central hole of 1.5 cm for the neck) was then applied to the males of the unpreened group and left with the neck collar for one day, during which the control males (preening group) could clean their plumage. Preliminary observations on individually caged males confirmed that the soft plastic collar allowed the birds to carry out their normal activities: thirty min after the neck collar was removed, soiled males spent on average 22.5% (± 4.49 SE) of their time preening versus 12.8% (± 1.02 SE) before soiling (n = 6). This increased preening activity allowed the male to rapidly clean the plumage (see also results). An alternative experimental approach would have been to fit the neck collar on a group of birds and allow them to get naturally dirty. However, this is a difficult to achieve in captivity, where food is provided ad libitum, and birds spend most of their time perching and resting. Most of the activities that probably soil the plumage, such as food searching, avoiding predators, brooding eggs or young etc., are prevented in these conditions. In preliminary trials we found that, under such unnatural conditions as those inevitably associated with captivity, birds kept with the neck collar for 2 days did not show any appreciable change in plumage condition. Even assuming that keeping birds for longer time with neck collars would eventually result in appreciable soiling in captive conditions, it is likely that this will also affect their behaviour, making then difficult to interpret the results of mate choice experiments. Instead, the artificial soiling we used allowed us to treat the two groups of birds in a similar way with respect to the time the neck collar was worn.

Colour measurements were taken on the breast from each male of the two treatment groups (preened and unpreened) before soiling and 1 day after soiling. The reflectance in the 320-700 nm range was measured with an Ocean Optics, Inc. USB 2000 spectrometer and a deuterium-halogen light source. Reflectance spectra were generated in proportion to a WS-2 white reference tile. For each individual male three measurements were taken, removing the probe between each scan. The three measurements were averaged for every male. We used three objective indices of the three main colours perception (HAILMAN 1977), which have been used in previous studies on birds (e.g. HUNT et al. 1999, KEYSER & HILL 1999, SHELDON et al. 1999, ÖRNBORG et al. 2002, GRIFFITH et al. 2003), namely spectral intensity ("brightness"), as the sum of reflectance in the whole spectral range ($R_{320\text{-}700}$), spectral location, as the wavelength of peak reflectance ("hue", $\lambda_{(Rmax)}$), and spectral chroma. Although there are several ways to measure chroma, we used "UV chroma", ($R_{320\text{-}400}/R_{320\text{-}700}$) that addresses the specific importance of UV (e.g. ANDERSSON & AMUNDSEN 1997, ANDERSSON et al. 1998, SHELDON et al. 1999, GRIFFITH et al. 2003). The considered spectral range (320-700 nm) corresponds to the typical visual range of budgerigars (BOWMAKER et al. 1997). A repeated measure ANOVA was used to test the differences in colour parameters before and after the treatment in both groups (preened and unpreened males).

Effect of preening on female mate choice

Female choice in relation to male plumage condition was studied in a two choice chamber (2 × 0.5 m and 0.5 m high; Fig.1) in which a female was allowed to choose between a preened and a soiled male. A female was placed in the central chamber, with one stimulus male in each one of the side compartments (see below), and allowed to settle. Two opaque partitions prevented males and females from visually interacting during the acclimatisation period. A nest box, positioned in the middle of the central chamber, was provided to stimulate breeding conditions. After the end of the acclimatisation period, the opaque partitions were removed and the trial started. Partial opaque dividers on each side of the nest box prevented the males from visually interacting (see Fig. 1). Females were therefore unable to see the males when sitting in front of the nest box. To observe the males they had to actively move to the left or the right side of their sector. Water and food were provided in each of the three sectors. In order to reduce isolation stress, calls from the home aviaries were recorded and played during the experiments from a speaker positioned on the nest box (PEARN et al. 2001). The choice trials were carried out in the morning, between 08.00 and 11.00.

Stimulus males (n = 28) were soiled as above and put in the test apparatus the day before the female choice test. One group of stimulus males was prevented from preening with a neck collar (n = 14), whereas the other males were allowed to clean their plumage (n = 14). One hour before the experiment the neck collar was applied also to the preened birds and therefore both birds were wearing the neck collar during the choice test. The alternative would have been to present both males to the female without a neck collar. We excluded this possibility because soiled males start to preen as soon as the neck collar is removed. The female was then introduced into the apparatus in the morning and, as soon as she resumed normal behaviour, opaque partitions between males and females were substituted by a net and the trials commenced. Each female (n = 14) was given a choice of one male that was allowed to preen and one that was prevented from doing so. Both males were unfamiliar to the test female and were used only once. The position of the female was recorded every 30 sec for 10 min. The position of the soiled and clean male was alternated between trials with respect to the side (left or right) of the choice chamber. As a result, in half of the trials clean male was on the left side and in half on the right side. The proportion of times that the female was in the compartment near the clean male was used as an index of female prefer-

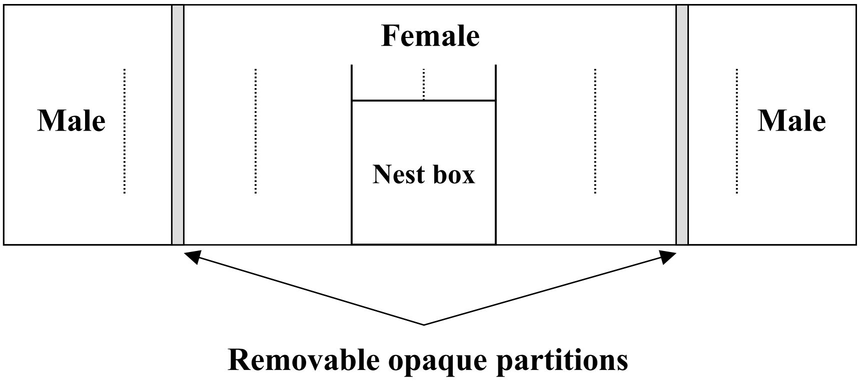

Fig. 1. — Top view of the mate choice chamber. The female was placed in the central chamber, one preened (clean) and one unpreened (soiled) male on each side. The opaque walls on each side of the nest box reduced the possibility that males interacted and females could concurrently see both males. The four dotted lines in the scheme indicate the position of perches.

ence. We tested whether females prefer the clean male, i.e. spend more time near the clean male than expected by chance. We discarded three trials during which the female preened or did not move during the entire trial.

Statistical methods

We used SPSS 12.0 to perform statistical tests. All probabilities are two-tailed and, if not otherwise stated, means ± SE are given.

RESULTS

The reflectance spectrophotometry of the breast feathers from twelve live blue-type budgerigars, before soiling, is reported in Fig. 2. Soiling determined a decrease in plumage reflectance in the budgerigars that were prevented from preening, whereas the budgerigars that could preen recovered their initial reflectance spectrum (Fig. 3). The change in reflectance in the two groups (preened and unpreened) reported in Fig. 3 suggests that, although the decrease of reflectance affected the whole spectrum measured, it was more pronounced in the short wavelength of the spectrum. A repeated measure ANOVA revealed that, although there was a significant overall difference in brightness before and after the experiment (time, $F = 13.46$, $df = 1,10$, $P = 0.004$), brightness changed differently in the two treatment groups according to whether or not males had been allowed to preen (treatment group, $F = 7.20$, $df = 1,10$, $P = 0.023$; interaction, $F = 11.50$, $df = 1,10$, $P = 0.007$). In particular, the soiled plumage of males prevented from preening revealed lower spectral intensity than before the treatment, whereas males that were allowed to preen restored the spectral intensity observed before soiling and approached the

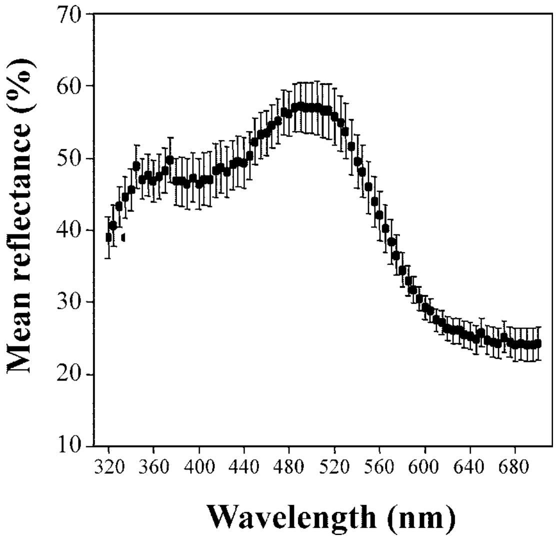

Fig. 2. — Average reflectance spectrum of male blue-type budgerigar breast feathers (n = 12). Means ± SE are given.

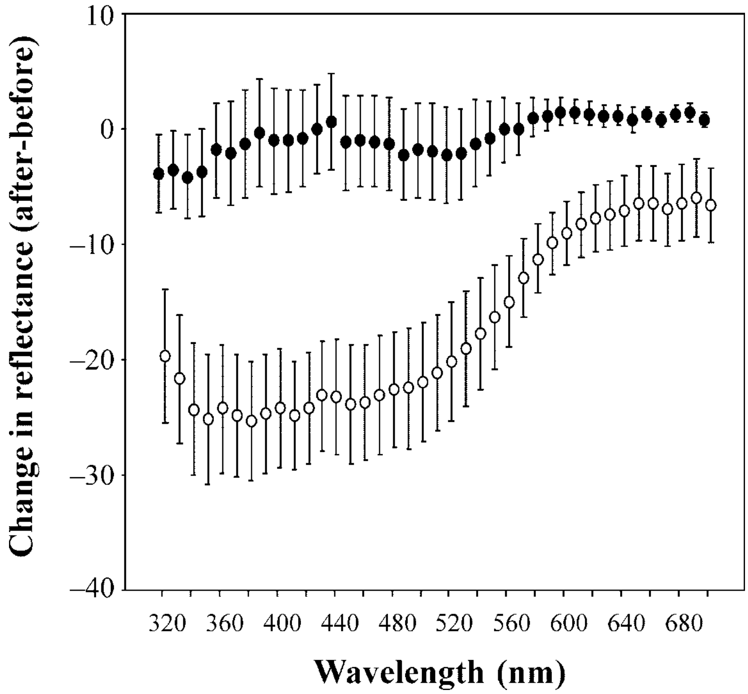

Fig. 3. — Change in reflectance of the breast feathers obtained by the subtraction of the average reflectance values before soiling and one day after soiling when males have been allowed to preen (n = 6, filled points) or prevented from preening (n = 6, open points). Mean change (± SE) is given.

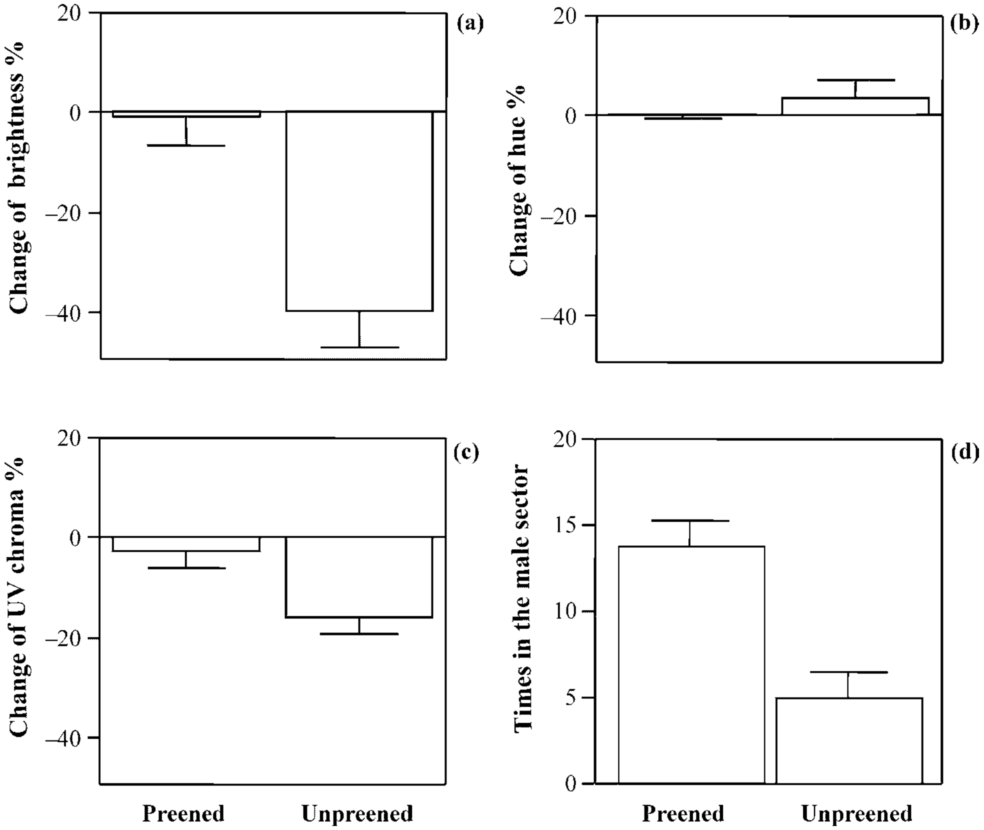

Fig. 4. — Change of (a) brightness, (b) hue and (c) UV chroma of the plumage of males that were allowed to clean, or prevented from cleaning, their plumage after the soiling treatment. Changes are expressed as [(value after – value before)/value before * 100]. (d) Results of a female choice test in which females (n = 11) could choose between a preened and an unpreened male. Female preference is expressed as the number of stays in the side compartment adjacent the preened and unpreened male, respectively (see Fig. 1). Bars represent mean ± SE.

values before the treatment (Fig. 4a). The hue ($\lambda_{(Rmax)}$) was not significantly affected by soiling and preening (time, F = 1.103, df = 1,10, *P* = 0.32; treatment group, F = 1.81, df = 1,10, *P* = 0.21, Fig. 4b). The proportion of UV reflectance to the total reflectance (UV chroma) changed significantly between before and after the treatment (time, F = 17.381, df = 1,10, *P* = 0.002, treatment group, F = 0.32, df = 1,10, *P* = 0.86). The significance of the interaction term (F = 7.608, df = 1,10, *P* = 0.02) suggests that the decrease of the UV reflectance relative to other spectral ranges was more pronounced in the group of males which were prevented from preening (Fig. 4c). A chroma measure based on the entire spectrum, $(R_{max}\text{-}R_{min})/(R_{320\text{-}700})$, did not reveal a significant effect of soiling and preening (time, F = 3.00, df = 1,10, *P* = 0.11; treatment group, F = 2.88, df = 1,10, *P* = 0.12; interaction term, F = 0.18, df

= 1,10, P = 0.68), supporting the view that the change in chroma was particularly pronounced in the UV spectrum range.

During the 10-min choice tests, females spent only 6.36 ± 2.53% of their time in the central, no-choice sector (frequency of stays = 1.27 ± 0.61, range = 0-4). Females spent significantly more time on the side of the preened male (frequency of stays = 13.73 ± 1.42) than on the side of the soiled male (frequency of stays = 5.00 ± 1.35; paired t-test, t = 3.20, n = 11, P = 0.01; Fig. 4d). Similar results were obtained when the proportion of stays near the preened male over the total stays in the two choice zones was compared to a random expectation (expected proportion = 0.5, one sample t-test, t = 3.21, P = 0.009).

DISCUSSION

Our results indicate that plumage reflectance can be influenced by soiling if preening is impaired. In the conditions tested in this study, males which were soiled and prevented from preening showed a pronounced and significant decrease in overall brightness. In contrast, males that were allowed to preen were able to restore the normal reflectance spectrum in a relatively short time and the spectrum of the preened birds approximated the reflectance values observed before the soiling treatment. Soiling reduced the plumage reflectance along the entire spectrum, but more strongly below 500 nm, as suggested by the significant change in the UV chroma in the unpreened group. We do not know whether the more pronounced reduction of short wavelength reflectance is a consequence of the soiling method used in this study or a general feature of soiled plumage. It is important to note, however, that a similar pattern of reflectance reduction has also been found in a study on free-ranging blue tits in which the authors compared freshly moulted plumage with 6-months old plumage (Örnborg et al. 2002). In the blue tit study, the reduction of UV chroma ranged between – 10% and – 15% (see table 2 in Örnborg et al. 2002), a value comparable to the – 20.3% ± 10.6 SD observed in budgerigars (Fig. 4c). Örnborg et al. (2002) suggested, on the basis of their personal observations, that dirt and fat absorb most at shorter wavelengths, suggesting that the reduction of the UV chroma was probably due to soiling, something confirmed by our results with budgerigars. Together these two studies suggest that feather condition (Örnborg et al. 2002) and preening (this study) influence plumage reflectance spectrum by reducing the overall brightness. Furthermore, plumage condition affected the shape of the spectrum caused by a more pronounced reduction of the reflectance in the short wavelengths. Plumage maintenance, at least partly mediated by preening, may therefore be particularly important for the efficiency of UV feather ornaments.

Our mate choice experiment provided evidence that female budgerigars prefer clean males. It seems unlikely the observed preference for the preened male was confounded by the female trying to avoid the unpreened male, although this hypothesis cannot be completely discounted. In fact, females spent very little time in the central, no-choice area where they could perch without interacting with the males. This is the first experiment, to our knowledge, testing the effect of preening on plumage reflectance and female choice. We do not know exactly what was the cue used by the females for their mate choice. Females may pay attention, for example, to the overall brightness reduction, the reduction in a specific part of the spectrum, or the change in chroma. Under the condition used in this experiment, the reduction of reflectance in the long wavelength part of the spectrum was smaller than in the short wavelength range. Since female budgerigars base their mate choice on the male UV reflectance (PEARN et al. 2001, although it must be noted that mate preference for the different colours has never been studied in blue budgerigars), one may speculate that UV ornaments have a specific role in mate choice (OWENS & HARTLEY 1998, HAUSMANN et al. 2003) because they signal plumage maintenance and a male's actual condition (see below). Further experiments are necessary to investigate this intriguing possibility. In particular, further female choice tests may reveal whether females discriminate between soiled males and males whose UV reflectance has been reduced using UV-blocking filters (e.g. BENNETT et al. 1997).

Why should a female prefer clean males? One reason may be that males in poor condition are more likely to soil their plumage and/or can devote less time to plumage maintenance (if, for instance, plumage maintenance is costly and its costs are condition-dependent, ZAHAVI 1975). Male budgerigars spend about 10% of their time preening in captivity (authors' unpublished observations). This figure is in the range reported for other bird species (COTGREAVE & CLAYTON 1994). Preening behaviour, as an important part of the daily time-budget, may therefore represent a cost if it reduces the time available for other activities. Indeed, great tits (*P. major*) experimentally infested with the hen flea (*Ceratophyllus gallinae*) reduced their sleeping time significantly so as to engage in nest sanitation behaviour (CHRISTE et al. 1996). Males in bad territories or those subject to parasites or diseases may therefore not be able to maintain their plumage in an optimal condition. One may argue that our experiment, where preening was completely suppressed, has tested an extreme condition. However, circumstances in which preening is severely constrained are also observed in nature. For example, spring migrants found in very bad condition on small islands (PILASTRO & SPINA 1997) have a visibly deteriorated plumage, with disarranged and dirty feathers (A. PILASTRO unpublished observations). During the breeding season, when time budgets are tight, birds may not be able to increase their preening time even in the presence of ectoparasites (e.g. MØLLER 1991, CHRISTE et al. 1996, TRIPET et al. 2002). Finally, some diseases can themselves cause a reduction of time devoted to preening (e.g. YORINKS & ATKINSON 2000).

In conclusion, our results provide experimental evidence that feather ornaments reflecting in the short wavelength spectrum are particularly sensitive to soiling and influenced by plumage maintenance (see also ÖRNBORG et al. 2002). Furthermore, our findings suggest that plumage soiling affects female choice and that this effect is removed once preening is allowed. Further investigation is necessary to confirm the generality of the link between soiling, preening and female choice, ideally by comparing different soiling conditions in a broader taxonomic range.

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