

RESEARCH PAPERS

Is Preening Behaviour Sexually Selected? An Experimental Approach

Matteo Griggio & Herbert Hoi

Konrad Lorenz Institute for Ethology, Vienna, Austria

Correspondence

Matteo Griggio, Dipartimento di Biologia,
Università di Padova, Via U. Bassi 58/B,
I-35131 Padova, Italy.
E-mail: matteo.griggio@unipd.it

Received: March 27, 2006

Initial acceptance: April 4, 2006

Final acceptance: April 30, 2006 (J. Schneider)

doi: 10.1111/j.1439-0310.2006.01270.x

Abstract

Elaborate or colourful feathers are important traits in female mate choice in birds but little attention has been given to potential costs of maintaining these traits in good condition with preening behaviour. Recent studies indicate that the time and energy required to maintain ornamental plumage in good condition reinforces the honesty of plumage trait. It has been proposed that some behaviours, whose primary function is not to transfer information, can also evolve as signalling components. Here we investigate whether the preening behaviour intensity has a signalling component: we hypothesized that if only high quality males can invest a lot of time in preening, this behaviour may be used by females as a quality signal (attractive preening hypothesis). We tested this hypothesis by using female budgerigars in mate-choice tests in captivity. We tried to experimentally manipulate the preening behaviour of two groups of budgerigar males (treatment and control group). The proportion of time in which treated males preened in front of females was statistically higher than for control males, however, females spent similar amounts of time with treated males and control males. Moreover, males did not show significant quantitative changes in preening (for both groups) when females were present, suggesting that male budgerigars did not use this behaviour to convey information. These results are inconsistent with the 'attractive preening' hypothesis which predicts that preening behaviour itself provides information on condition and is used in female choice.

Introduction

Comfort behaviour, in particular preening, is one aspect of self maintenance behaviour which has not attracted many investigations. Preening requires time which may result in a temporal trade-off between investment in preening and other activities (Redpath 1988; Cucco & Malacarne 1997). Furthermore, preening produces public information which may vary depending on the receivers, i.e. the information transferred may differ for conspecific group members, predators or potential mates (Danchin et al. 2004). In birds for example, to maintain the

plumage in good condition is essential for flight but also for mate choice. There is evidence for the importance of ornamental traits in mate choice and that females benefit by choosing a male based on the expression of elaborate or colourful plumage ornaments (for a review see Andersson 1994). Conspicuous plumage signals are assumed to provide the choosy sex with information about potential mates. Many studies have demonstrated that conspicuous plumage ornamentation correlates with aspects of individual quality such as parasite resistance, immunocompetence, diet and social status (e.g. Zahavi 1975; Hill & Montgomerie 1994; Swaddle & Witter

1994; Pärt & Qvarnström 1997; McGraw & Hill 2000). Increased conspicuousness due to plumage ornaments may also act as a handicap, because it elevates predation risk (Andersson 1994). Associated with the production of plumage ornaments could be their maintenance costs. Birds spend time and energy to maintain the ornamental traits in good condition, removing the oiling and dirt from the feathers or control ectoparasites (Cotgreave & Clayton 1994) resulting in a temporal trade-off between investment in plumage maintenance and other activities, such as foraging and vigilance (Redpath 1988; Cucco & Malacarne 1997). Indeed, in average, bird species spent 9.2% of their daily time budget on maintenance behaviour (Cotgreave & Clayton 1994). A trade-off in time and energy is also supported by the fact that wild individuals spent 8.7% whereas captive individuals spent 15.75% of their time on maintenance behaviour (Walther & Clayton 2005). If grooming behaviour reinforces the honesty of plumage traits it consequently should be used in mate choice as well. Despite the potential importance of preening in plumage maintenance, only recently has this behaviour received attention. Walther & Clayton (2005) found in a comparative study, that species with more elaborate plumage ornaments spend more time in maintenance behaviour. On one hand, this 'high maintenance' cost reinforces the honesty of ornamental plumage; on the other hand, the preening behaviour itself could be sexually selected. The 'attractive preening' hypothesis predicts that preening may be used by females as a quality indicator because only high quality males can invest a lot of their time in preening. Consequently, males would exhibit this behaviour more often when observed by a female. In contrast, if males adjust preening investment according to infestation rate with ectoparasites the 'preening avoidance' hypothesis, predicts that females would reject heavily preening males to avoid infestation with parasites and males would consequently try to avoid preening in presence of females. In Seychelles warblers (*Acrocephalus sechellensis*) and barn swallows (*Hirundo rustica*), males preened more than females, but there was no relation to feather mite loads (Møller 1991). This may suggest that preening behaviour is necessary to keep the plumage neat and convey an honest signal to females (Dowling et al. 2001). Female rock doves (*Columbia livia*), i.e. prefer clean over lousy males but their choice is not based on preening intensity (see Clayton 1990). So, there is no evidence for the importance of preening behaviour in mate choice.

In this study, we experimentally manipulated preening behaviour in budgerigars (*Melopsittacus undulatus*) to examine the importance of preening for female mate choice. The socially monogamous budgerigar is an ideal model species for such a study. First, it was already demonstrated that plumage properties, and in particular UV colours, have a relevant role in mate choice (Pearn et al. 2001, 2003). Secondly, there is evidence (Zampiga et al. 2004) that females are able to discriminate between preened and unpreened males, and that soiling affects plumage reflectance particularly in the UV range. However, an experimental test is needed to determine whether this conveys information on individual condition. Third, budgerigars are social animal, and animals in social group may change their behaviour depending on the presence of conspecific, this is called 'audience effect' (e.g. Gyger et al. 1986). Captive male budgerigars demonstrate an 'audience effect', indeed they are significantly more likely to court extra-pair females when their current mates are positioned behind an opaque barrier, than when couples are within sight of each other (Baltz & Clark 1997). This indicates that male budgerigars adjust their behaviour depending on the presence of conspecifics. The two main questions of our investigation are: (1) do females choose males according to preening investment?, and (2) do males use this behaviour to advertise their quality to females which is an assumption for the 'attractive preening' hypothesis?

Methods

Manipulation of Preening Behaviour

In December 2004, 40 male blue-type adult (over 1 yr old) budgerigars were selected randomly from three indoor aviaries where females were present. Males were divided in two groups (treatment and control group), and they were placed in indoor singular cages (50 × 50 × 50 cm); seeds, lettuce, carrots and water were available ad libitum before and during the experiments. We applied white wheat flour (approx. 1.5 g) under the breast feathers (approx. on a 3 × 3 cm area) of 20 males (treatment group) and we disarranged the breast feathers in other 20 males (control group). The control males experienced the same motions for the same amount of time of the treated males. Twenty minutes after the manipulation we recorded the preening behaviour every 15 s for 30 min.

Female Mate-Choice and Preening Behaviour

In December 2004 and in March 2006, a total of 33 female blue-type adult (over 1 yr old) budgerigars were housed indoors in single-sex groups under 14:10 L:D photoperiod. Seeds, lettuce, carrots and water were available ad libitum, and several nest boxes were present in order to stimulate breeding condition. All the females developed the brown cere, signalling their readiness to breed (Juniper & Parr 1998). Sixty-six stimulus males (56 were used in 2004 and 10 in 2006) were randomly allocated to the treatment or control group. We conducted female mate-choice trials in a two choice chamber ($2 \times 0.5 \times 0.5$ m; Fig. 1). Females were placed in the central chamber in which they were allowed to move between two simultaneously presented males situated in adjacent 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 (Fig. 1). Moreover, a nest box was provided in the middle of the central chamber in order to induce breeding behaviour. Water and food were provided to all animals before and during the experiments. Calls were recorded in aviaries, where both males and females were present, and played back during the experiments from a speaker situated in the centre of the experimental room to reduce any isolation stress (Pearn et al. 2001). 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. On the afternoon before the stimulus males were presented to females, males were placed in the two side compartments to allow habituation to the cages. The experimental observations were carried out between 08.00 and 11.30 hours. The female was introduced in the apparatus in the morning (approx. 2 h before the trial commenced); two opaque partitions between female and males were erected in order to prevent visual contact between individuals. Stimulus males were manipulated in the same way

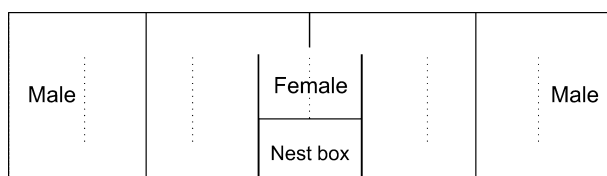


Fig. 1: Plain view of the mate-choice apparatus. The dashed lines in the scheme indicate the position of perches

described for the Manipulation of preening behaviour (see above). Twenty minutes after the manipulation, opaque partitions between the female and the males were substituted by a wire mesh. We then recorded the position of the female and the preening behaviour of males every 15 s for 30 min (Vos 1995). During the observation period females moved back and forth between the males several times; many times females initiated body contact with males by clinging the wire mesh. Males often performed display behaviours in front of females, such as head bobbing. In eight trials, females did not visit any of the two males or males did not preen in front of females: these trials were therefore discarded. In total we performed 25 successful trials (20 in 2004 and five in 2006) in which females observed treated males preening. No female and no stimulus male were used more than once. All birds were unfamiliar with each other because they came from different visually and acoustically separated aviaries. Before the experiment, we took standard measurements of wing length and body mass for all males. We did not detect any difference between the two groups of stimulus males used in the 25 successful trials in weight (Student's t-test: $t = 0.28$, $df = 48$, $p = 0.78$) and wing length ($t = 0.27$, $df = 48$, $p = 0.79$). Colour measurements were taken on the breast from the 20 males before the meal was applied and after the treatment and the same for all the control males. The reflectance in the 320–700 nm range was measured with an Ocean Optics, Inc. USB 2000 spectrometer and a deuterium–halogen source (DH-2000). The light source illuminated the feathers through an optical fibre and was reflected through a plastic window cut at 45° . A software package (Spectrawin 4.2, Ocean Optics, Eerbeek, The Netherlands) computed reflectance spectra relative to a white reference tile (SW-2). For each individual male, five measurements (each spectrum was averaged from five scans) were taken removing the probe between each measurement. We then averaged the five measurements for the males before and after the manipulation. We quantified colour using three standard parameters of reflectance spectra: hue (λ_{Rmax}), UV chroma ($R_{320-400}/R_{320-700}$) and intensity ($R_{320-700}$) of each individual. These parameters have been used in previous studies on birds (Hunt et al. 1999; Sheldon et al. 1999; Griffith et al. 2003).

All the results are presented as mean \pm SE. All tests are two-tailed. We performed statistics using SPSS 12.0 (Norušis 1993). Analyses were checked to ensure that they met the assumptions of parametric statistics. A repeated measure ANOVA was used to test

the differences in colour parameters before and after the treatment (time) in both groups of control and treated males (treatment group). We measured the time females spent on each side (left area, no choice area, right area; Fig. 1). Preference for right or left side (in front a particular male), was regarded as mate preference.

Results

Manipulation of Preening Behaviour

Treated males spent $20.16 \pm 2.18\%$ (range: 9.2–45, $n = 20$) of their time in feather maintenance, and the control males spent $10.00 \pm 1.46\%$ (range: 2.5–25, $n = 20$), a difference that was significant ($t = 3.19$, $df = 38$, $p < 0.001$). Moreover, treated males generally preened themselves during all the behavioural observation period; this suggests that males were not able to remove all of the meal in a short time.

Female Mate-Choice and Preening Behaviour

A repeated measure ANOVA did not detect any significant difference in colour parameters before and after the treatment in both groups of males: hue (time, $F = 0.97$, $df = 1,24$, $p = 0.34$; treatment group, $F = 2.90$, $df = 1,24$, $p = 0.10$; interaction, $F = 0.04$, $df = 1,24$, $p = 0.853$), UV chroma (time, $F = 3.39$, $df = 1,24$, $p = 0.08$; treatment group, $F = 1.70$, $df = 1,24$, $p = 0.21$; interaction, $F = 2.28$, $df = 1,24$, $p = 0.144$), and intensity (time, $F = 0.25$, $df = 1,24$, $p = 0.62$; treatment group, $F = 0.17$, $df = 1,24$, $p = 0.68$; interaction, $F = 1.81$, $df = 1,24$, $p = 0.19$). We did not detect any significant differences on the preening behaviour between the males used in Manipulation of preening behaviour and those used in the female mate-choice experiment (Student t -test, treated: $t = 0.30$, $df = 43$, $p = 0.76$; control: $t = 0.28$, $df = 43$, $p = 0.78$). Females spent on average $9.63 \pm 2.64\%$ (range 0–53%) of their time within the no choice area (Fig. 2). Twenty-four of 25 females showed a clear preference for a particular males (paired t -test: $p < 0.04$), but selected males were equally distributed in the two groups balancing the total female preference (Fig. 2). Indeed, despite the fact that the proportion of time in which treated males preened in front of females was statistically higher than control males (treated males: $20.45 \pm 2.89\%$, range: 5–59%; control males: $7.18 \pm 1.69\%$, range: 0–32%; $t = 3.08$, $df = 48$, $p = 0.003$, Fig. 3), females spent similar amounts of time with treated males (mean \pm SE: $43.67 \pm 4.0\%$;

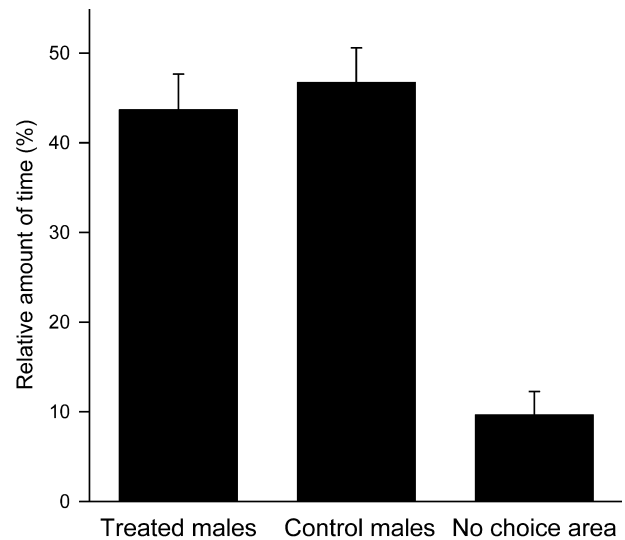


Fig. 2: Results of the female mate-choice experiment, showing the percentage of time (mean \pm SE) spent by female in the no choice area, near the more preening male (treated group) and less preening male (control group), placed on each side of the choice chamber

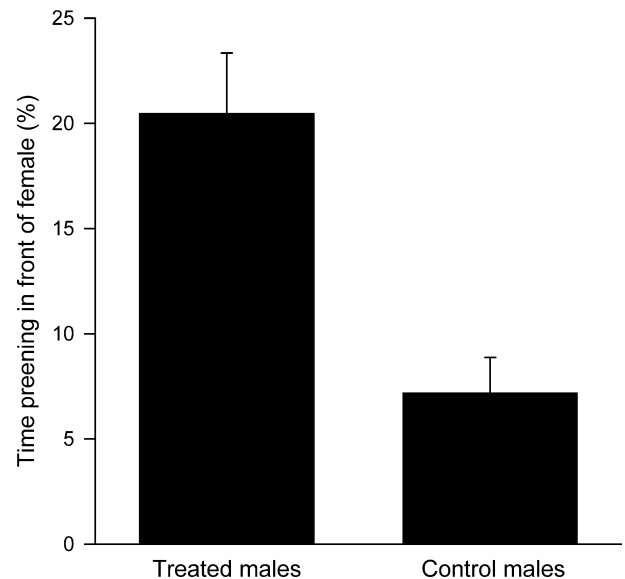


Fig. 3: Percentage of time (mean \pm SE) spent by males in preening in front of the female during the female mate-choice experiment

range: 15–88%, Fig. 2) and control males (mean \pm SE: $46.70 \pm 3.89\%$; range: 12–85% Fig. 2; paired t -test, $t = 0.34$, $df = 24$, $p = 0.74$). The power of the paired t -test with our data is $>95\%$, with a critical two-tailed α -level of 0.05. We had therefore enough power ($>80\%$; convention suggested by Cohen 1988) to find a significant female preference if it existed in our sample. To examine whether the

presence of the female influenced male preening behaviour we compared the time spent preening by males when females were present in their choice area with the time spent preening when females were not present in their choice area. We examined this in both groups and there was no evidence that female presence had an effect (paired t-test; treated: $t = -0.42$, $df = 24$, $p = 0.69$; control: $t = -0.47$, $df = 24$, $p = 0.642$).

Discussion

We found a significant effect of our treatment on preening behaviour but no female preference in relation to male preening behaviour. Females showed preferences for specific males but these were independent of our treatment. Comparing each group in the two different situations (presence or absence of females), we could demonstrate that female presence did not influence the occurrence of preening behaviour.

The idea that female mate choice might be driven, not only by ornaments or courtship behaviours but also by other particular behaviours, has been suggested several times (e.g. Reyer 1986; Freeman-Gallant 1997; Lotem et al. 1999). Although preening is a likely candidate to have a signalling component, there is, to our knowledge, no study in birds investigating whether female mate choice may include or is based on preening behaviour intensity. Despite the large number of stimulus males and response females, there was no evidence for budgerigar females to consider male preening when choosing a potential partner. Furthermore, males did not show significant quantitative changes in preening (for both groups) when females were present, suggesting that male budgerigars did not use this behaviour to convey information about their current condition. Our study, however, also does not support the 'preening avoidance' hypothesis which would predict that females avoid preening males. One might argue that a period of 30 min of behavioural observation were not sufficient to know if females had made a definitive choice, but using the same, or even a shorter time period (Zampiga et al. 2004), we found a clear female preference in this species (M. G. & H. H. unpubl. obs.).

Studies on birds have provided evidence that females benefit by choosing a male based on expression of colourful feathers. For ornamental traits to be honest, they must be costly to produce or maintain (Zahavi 1975; Grafen 1990). Ornamen-

tal plumage coloration results from either pigments deposited in feathers (such as carotenoids or melanins, e.g. Hill & Brawner 1998; Olson & Owens 1998) or feather microstructure (giving for example ultraviolet colours, Andersson 1999). Honesty may be therefore influenced by the type of pigment used. For example, melanin-based ornamental coloration seems to be under social control: in a number of species melanin-based traits function as badges of social status (the 'status signalling hypothesis' Rohwer 1975, for a review see Senar 1999). On the other hand, carotenoid-based ornamental coloration correlates with some aspect of individual quality such as parasite resistance, immunocompetence and diet (for a review see Olson & Owens 1998). Lastly, UV colorations seem to signal developmental stability of an individual (Andersson 1999) and correlate with nematode parasite infection. Indeed, in red grouse (*Lagopus lagopus*) brighter UV in combs (a sexually selected trait) reflect the intensity of infection by a main nematode parasite (Mougeot et al. 2005). Although all these plumage traits already function as reliable signals of individual quality, preening may offer a reinforcement to maintain the honesty of a trait already expensive to produce or may be important for the efficacy of feather signals (Zampiga et al. 2004). Studies of sexual selection should take into account variation in the ability of individuals to keep ornaments in good condition (Barbosa 1996; Clayton et al. 2005; Walther & Clayton 2005). Preening and maintaining the plumage in good condition, removing dirt and fat, ordering the plumage and reducing the ectoparasite load may affect the reflectance properties of colour plumage and in turn directly affect male attractiveness. The honesty of the final result is guaranteed by the time devoting for the preening behaviour. Indeed, recent studies indicate that the time and energy required to maintain the ornamental plumage in good condition reinforce the honesty of plumage trait (Zampiga et al. 2004; Walther & Clayton 2005).

Nonetheless, more experiments and field work is needed to clarify our understanding of the possible relationship of preening behaviour and mate choice, before discarding the 'attractive preening' hypothesis.

Acknowledgements

We are grateful to R. H. Wagner, J. Schneider and two anonymous referees for their constructive comments on this manuscript.

Literature Cited

- Andersson, M. 1994: Sexual Selection. Princeton Univ. Press, Princeton, NJ.
- Andersson, S. 1999: Morphology of UV reflectance in a whistling-thrush: implications for the study of structural colour signalling in birds. *J. Avian. Biol.* **30**, 193–204.
- Baltz, A. P. & Clark, A. B. 1997: Extra-pair courtship behaviour of male budgerigars and the effect of an audience. *Anim. Behav.* **53**, 1017–1024.
- Barbosa, A. 1996: Relationship between bill morphology and preening behaviour in waders. *Ethol. Ecol. Evol* **8**, 291–296.
- Clayton, D. H. 1990: Mate choice in experimentally parasitized rock doves: lousy males lose. *Am. Zool.* **30**, 251–262.
- Clayton, D. H., Moyer, B. R., Bush, S. E., Jones, T. G., Gardiner, D. W., Rhodes, B. B. & Goller, F. 2005: Adaptive significance of avian beak morphology for ectoparasite control. *Proc. R. Soc. Lond. B* **272**, 811–817.
- Cohen, J. 1988: Statistical Power Analysis for the Behavioral Sciences. Lawrence Erlbaum Associates, Hillsdale, NJ.
- Cotgreave, P. & Clayton, D. H. 1994: Comparative analysis of time spent grooming by birds in relation to parasite load. *Behaviour* **131**, 171–187.
- Cucco, M. & Malacarne, G. 1997: The effect of supplemental food on time budget and body condition in the black redstart *Phoenicurus ochruros*. *Ardea* **85**, 211–221.
- Danchin, E., Giraldeau, L. A., Valone, T. J. & Wagner, R. H. 2004: Public information: from nosy neighbors to cultural evolution. *Science* **305**, 487–491.
- Dowling, D. K., Richardson, D. S. & Komdeur, J. 2001: No effects of a feather mite on body condition, survivorship, or grooming behavior in the Seychelles warbler, *Acrocephalus sechellensis*. *Behav. Ecol. Sociobiol.* **50**, 257–262.
- Freeman-Gallant, C. R. 1997: Parentage and parental care: consequences of intersexual selection in Savannah sparrows? *Behav. Ecol. Sociobiol.* **40**, 395–400.
- Grafen, A. 1990: Biological signals as handicap. *J. Theor. Biol.* **144**, 517–546.
- Griffith, S. C., Örnborg, J., Russell, A. F., Andersson, S. & Sheldon, B. C. 2003: Correlations between ultraviolet coloration, overwinter survival and offspring sex ratio in the blue tit. *J. Evol. Biol.* **16**, 1045–1054.
- Gyger, M., Karakashian, S. J. & Marler, P. 1986: Avian alarm calling: is there an audience effect? *Anim. Behav.* **34**, 1570–1572.
- Hill, G. E. & Brawner, W. R. III 1998: Melanin-based plumage coloration in the hose finch is unaffected by co-cidial infection. *Proc. R. Soc. Lond. B* **265**, 1105–1109.
- Hill, G. E. & Montgomerie, R. 1994: Plumage colour signals nutritional condition in the hose finch. *Proc. R. Soc. Lond. B* **258**, 47–52.
- Hunt, S., Cuthill, I. C., Bennett, A. T. D. & Griffiths, R. 1999: Preferences for ultraviolet partners in the blue tit. *Anim. Behav.* **58**, 809–815.
- Juniper, T. & Parr, M. 1998: Parrots – A Guide to the Parrots of the World. Pica Press, Robertsbridge, East Sussex, UK.
- Lotem, A., Wagner, R. H. & Balshine-Earn, S. 1999: The overlooked signaling component of nonsignaling behavior. *Behav. Ecol.* **10**, 209–212.
- Møller, A. P. 1991: The preening activity of swallows, *Hirundo rustica*, in relation to experimentally manipulated loads of haematophagous mites. *Anim. Behav.* **42**, 251–260.
- McGraw, K. J. & Hill, G. E. 2000: Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proc. R. Soc. Lond. B* **267**, 1525–1531.
- Mougeot, F., Redpath, S. M. & Leckie, F. 2005: Ultra-violet reflectance of male and female red grouse, *Lagopus lagopus scoticus*: sexual ornaments reflect nematode parasite intensity. *J. Avian. Biol.* **36**, 203–209.
- Norušis, M. J. 1993: SPSS for Windows Base System User's Guide Release 6.0. SPSS, Chicago.
- Olson, V. A. & Owens, I. P. F. 1998: Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol. Evol.* **13**, 510–514.
- Pärt, T. & Qvarnström, A. 1997: Badge size in collared flycatchers predicts outcome of male competition over territories. *Anim. Behav.* **54**, 893–899.
- Pearn, S. M., Bennet, A. T. D. & Cuthill, I. C. 2001: Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*. *Proc. R. Soc. Lond. B* **268**, 2273–2279.
- Pearn, S. M., Bennet, A. T. D. & Cuthill, I. C. 2003: The role of ultraviolet-A reflectance and ultraviolet-A-induced fluorescence in budgerigar mate choice. *Ethology* **109**, 961–970.
- Redpath, S. 1988: Vigilance levels in preening dunlin *Calidris alpina*. *Ibis* **130**, 555–557.
- Reyer, H. U. 1986: Breeder-helper interactions in the pied kingfisher reflect the costs and benefits of cooperative breeding. *Behaviour* **96**, 277–303.
- Rohwer, S. 1975: The social significance of avian winter plumage variability. *Evolution* **29**, 593–610.
- Senar, J. C. 1999: Plumage coloration as a signal of social status. In: Proceedings of the International Ornithological Congress, Vol. 22 (Adams, N. J. & Slotow, R. H., eds). BirdLife South Africa, Johannesburg, South Africa, pp. 1669–1686.
- Sheldon, B. C., Andersson, S., Griffith, S. C., Örnborg, J. & Sendecka, J. 1999: Ultraviolet colour variation influences blue tit sex ratios. *Nature* **402**, 874–877.

- Swaddle, J. P. & Witter, M. S. 1994: Food, feathers and fluctuating asymmetry. *Proc. R. Soc. Lond. B* **255**, 147—152.
- Vos, D. 1995: Sexual imprinting in zebra-finch females: do females develop a preference for males that look like their father? *Ethology* **99**, 252—262.
- Walther, B. A. & Clayton, D. H. 2005: Elaborate ornaments are costly to maintain: evidence for high maintenance handicaps. *Behav. Ecol.* **16**, 89—95.
- Zahavi, A. 1975: Mate selection – a selection for handicap. *J. Theor. Biol.* **53**, 205—214.
- Zampiga, E., Hoi, H. & Pilastro, A. 2004: Preening, plumage reflectance and female choice in budgerigars. *Ethol. Ecol. Evol.* **16**, 339—349.