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Blue, not UV, plumage color is important in satin bowerbird *Ptilonorhynchus violaceus* display

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Several studies have suggested that peak plumage reflectance in birds matches color preferences used in mate choice. We tested this hypothesis in adult satin bowerbird males that have a short-wavelength saturated blue-black plumage with a peak reflectance in the UV. We found that the chroma of the blue (405–480 nm), but not the peak reflecting UV (320–400 nm) portion of the male plumage spectrum was significantly correlated with male mating success. A plot of correlation coefficients between male mating success and plumage saturation showed a well-defined peak in the blue. This suggests that: 1) blue plumage coloration is more important in mate choice than UV or other colors, and 2) that there is a mismatch between the peak reflectance of the plumage of male satin bowerbirds and the range of plumage wavelengths that are correlated with male mating success. This indicates that it is not safe to infer a role of UV or other colors in mate choice simply because of a peak in plumage reflectance.

Colorful plumage displays are among the most striking examples of sexually selected traits (Darwin 1871, Andersson 1994), and these displays are often highly elaborated in polygynous bird species (Oakes 1992, Johnsgard 1994). Specific colors are important for mate choice in many polygynous and sexually dimorphic species (e.g. Collias et al. 1979, Stein and Uy 2006, Siitari et al. 2007). Among the spectral colors, ultraviolet (UV) reflectance and perception is widespread in birds (Eaton and Lanyon 2003) and much attention has been given to the importance of UV plumage reflectance (e.g. Guilford and Harvey 1998). UV reflectance has been considered a ''special signal'' because of its suggested special suitability for short-range signaling, generally high contrast with backgrounds and invisibility to some predators (Silberglied 1977, Bennett and Cuthill 1994, Hausmann et al. 2003), and this has resulted in numerous studies investigating the role of UV in avian mate choice. In many avian species UV plumage coloration does affect male mating success (Andersson and Amundsen 1997, Andersson et al. 1998, Hunt et al. 1998, Pearn et al. 2001) and this has led to the suggestion that high UV reflectance indicates that it has an important role in mate choice (Hausmann et al. 2003). However, recent studies of species with UV reflecting plumage (Hunt et al. 2001, Ballentine and Hill 2003, Liu et al. 2007, Siitari et al. 2007) suggest that the proposed relationship between UV reflectance and plumage attractiveness does not hold in all cases.

In satin bowerbirds *Ptilonorhynchus violaceus*, adult males have an iridescent short-wavelength (UV-blue) saturated plumage with peak reflectance in the UV (Doucet and Montgomerie 2003a), and male courtship display involves rapid extensions of both wings that produce bright flashes likely visible to females standing in the bower. The sexually dimorphic plumage coloration and display of plumage during courtship suggests that it may be an important element of mate choice in satin bowerbirds. Although how plumage coloration affects mate choice has long been discussed in bowerbirds (Gilliard 1956, 1969, Diamond 1986, Kusmierski et al. 1993, Kusmierski et al. 1997, Endler et al. 2005, Borgia et al. 2007), previous studies of bowerbird plumage have not found a significant relationship between adult male plumage coloration and male mating success (Doucet and Montgomerie 2003a, Madden et al. 2004). Madden et al. (2004) found that male spotted bowerbirds that owned a bower had larger crests than both females and males that did not own a bower, but they did not find a relationship between crest size and male mating success and did not report any relationships between crest color and male mating success. Doucet and Montgomerie (2003a) found that bower quality and number of bower decorations were significantly correlated with the first principal component (PC1) of a multivariate plumage analysis. This suggested the possibility that plumage reflectance may be important in sexual signalling in satin bowerbirds. However, they used correlated proxies (bower quality and number of bower decorations) for male mating success and their PC1 included a mixture of UV and non-UV specific plumage variables (see methods). Therefore, it is unclear to what extent UV reflectance explains male attractiveness in their analysis and how plumage reflectance of any color is related to male mating success in satin bowerbirds.

Measuring the relationship between plumage color and mating success is complicated by the continuous nature of the bird visible portion of the plumage reflectance spectrum and it can be difficult determining which parts of this spectrum (if any) contribute to male mating success. Siitari et al. (2007) divided the spectrum from 320 to 700 nm into 20 nm segments and plotted the coefficients of the correlations between the average reflectance in each spectral segment and male mating success. They found a peak in correlation coefficients near 420 nm in the black grouse *Tetrao tetrix* and this was near the wavelengths of peak plumage reflectance. This approach offered a novel method to compare the relative strength of the relationship between plumage reflectance and male mating success for different spectral regions. We use a modified version of their approach to visualize the relationship between male mating success and plumage chroma across the entire avian visible spectrum in satin bowerbirds.

Previous studies of satin bowerbirds have shown a strong preference for blue decorations (Morrison-Scott 1937, Marshall 1954, Borgia 1985b, Borgia et al. 1987, Borgia and Keagy 2006, Wojcieszek et al. 2006). In a non-experimental study Wojcieszek et al. (2006) showed that frequently stolen decorations were darker blue and had higher UV reflectance than decorations that were not stolen, but a larger experimental study (Borgia 2008) found that males do not discriminate between UV blocked and control blue decorations, suggesting that UV has no role in decoration preferences. The relevance of UV reflectance in satin bowerbirds has also been suggested for male plumage display (Doucet and Montgomerie 2003a, b) and here we investigate the relationship between plumage color and male mating success with a particular focus on the UV and blue regions. In this analysis we address three questions: 1) is there a relationship between UV plumage color and male mating success, 2) is there a relationship between blue plumage color and male mating success, and 3) do spectral regions that show highest reflectance correlate significantly with male mating success?

Methods

Study site and general methods

This study was carried out in 2003 at Tooloom National Park (28° 28′S, 152° 25′E), NSW, Australia (Borgia 1985a). This site is located in a valley formed by Wallaby Creek and extends 1.5 km into a system of ridges formed by the creek's tributaries. All males used in this study were bower holders in full adult plumage and were previously banded with unique color band combinations (Borgia 1985a). Males were captured individually using baited traps at feeding sites prior to the start of the mating season for plumage reflectance measurement. Daily counts of decorations at the bowers and assessments of bower quality were averaged over the mating season (November 5th until December 21st) for each male (Borgia 1985b).

Video monitoring

All courtship and mating behaviors occur at bowers in satin bowerbirds (Marshall 1954, Borgia 1985b) and this provides the opportunity to accurately measure male mating success. We monitored bowers throughout the mating season (early November until late December) using an automated video monitoring system that is triggered by an infrared sensor when birds are present (Borgia 1995). Cameras at each bower were checked twice daily to ensure that video tapes were changed before they ran out and that battery voltages were sufficient to run the monitoring system, thus ensuring a complete record of courtship and mating behavior at these bowers. The number of copulations each male achieved during the mating season was scored from these videos and this provides an accurate ranking of male mating success (Reynolds et al. 2007).

Color measurements

We measured plumage reflectance using a S2000 spectrometer and PX-2 pulsed xenon light source (Ocean Optics, Dunedin, Florida, USA). The probe was maintained perpendicular to the feather surface to replicate the measurement geometry used in other reflectance studies of satin bowerbirds (Doucet and Montgomerie 2003a, b, Doucet et al. 2006). The white-standard used was PTFE tape (Andersson and Prager 2006, Delhey et al. 2008), layered to produce a uniform white surface whose spectral properties did not change when adding an extra layer. We took 5 spectral measurements from each male: 2 of the auriculars, 2 of the lesser wing coverts and 1 of the rump. The measurements for each individual were averaged across body regions (Doucet and Montgomerie 2003a) and the resulting spectra were smoothed using a Gaussian kernel prior to statistical analysis (Fig. 1). This spectral smoothing is a low-pass filter that removes high frequency noise in the data. This noise is due in part to the very small distance between points in the spectral sampling (~1/3 nm between data points). This smoothing does not change estimates of spectral saturation (chroma) or total reflectance (brightness) but does provide a better estimate of the location of the reflectance peak (hue) than does the raw spectral data (Montgomerie 2006).

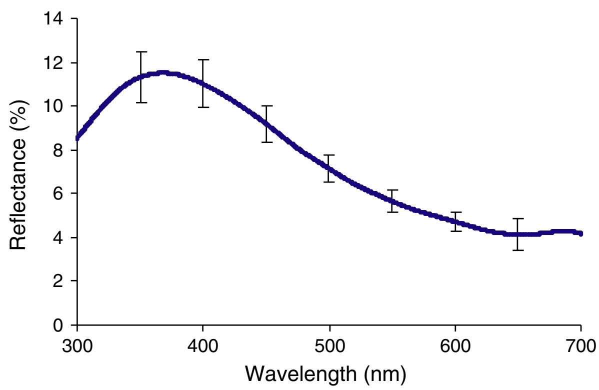

Figure 1. Mean reflectance spectra showing 95% CL plotted at 50 nm intervals of 13 bower holding adult males.

Statistical analyses

Since adult male satin bowerbird plumage reflects maximally in the UV portion of the spectrum (Doucet and Montgomerie 2003a), and because satin bowerbirds prefer blue decorations independent of UV reflectance (Borgia 2008) we tested for correlations between male mating success and the calculated chroma indices for both the UV wavelengths ($R_{320-400nm}/R_{320-700nm}$) as well as for the blue wavelengths ($R_{405-480nm}/R_{320-700nm}$) of male plumage reflectance (see Siitari et al. 2007).

Furthermore, to test the prediction that there was no relationship between mating success and plumage color in other parts of the spectrum outside the blue and UV spectral ranges we plotted the correlation coefficients of male mating success at 20 nm intervals across the entire avian visible spectrum (see Siitari et al. 2007). Since we wanted to characterize the variation among males in chroma, we standardized the intensity of each male's spectrum by dividing each data point by the total brightness. The resulting correlations are therefore between male mating success and the spectral saturation of male plumage at that wavelength interval. This approach is especially powerful as it allows the visualization of trends in the relationship between plumage reflectance and male mating success across the whole avian visible spectrum. A pattern in the strength of the correlation coefficients of these 20 nm intervals can indicate which part(s) of the spectrum is (are) likely to be important in female mate choice. If no comparisons outside the blue and UV ranges show a strong correlation to male mating success, then other colors are likely not important.

Paralleling previous work by Doucet and Montgomerie (2003a), we calculated the same overall plumage score to allow for comparison between studies. To do this we summarized the male reflectance spectra data using their measures for total brightness (mean $R_{300-700nm}$), UVV chroma ($R_{300-420nm}/R_{300-700nm}$), contrast($\lambda_{min} - \lambda_{max}$) and hue ($\lambda_{max}$). Here we used 300 rather than 320 nm as the lower limit for avian UV vision to replicate their analysis. All results are qualitatively the same using either UV cut-off. The first principal component from these four variables was used to calculate an overall plumage color score (Doucet and Montgomerie 2003a).

Nonparametric rank correlation tests were used because they are less sensitive to the strongly skewed distribution of matings among males in satin bowerbirds (Borgia 1985b). All tests of significance are two-tailed.

Results

We found a significant positive relationship between male mating success and the blue chroma of male plumage in the range between 405 and 480 nm ($r_s = 0.55$, $p = 0.05$, $n = 13$). No relationship was found with UV chroma ($r_s = 0.20$, $p = 0.52$, $n = 13$). Additionally, when we plotted the correlation coefficients between male mating success and the 20 nm spectral intervals we found a peak in the blue wavelengths and much lower correlation coefficients for wavelength ranges in other parts of the spectrum suggesting that UV and reflectance in other parts of the spectrum are not important in affecting male mating success (Fig. 2).

To compare our data to the previous study of satin bowerbird plumage (Doucet and Montgomerie 2003a), we calculated the same overall plumage score. This was the first principal component (PC1) of an analysis including total brightness, UVV chroma, contrast and hue (see methods for description of variables). The loadings of PC1 differed between the studies (Table 1). We did not find a significant relationship between this PC1 color score and male mating success ($r_s = 0.18$, $p = 0.55$, $n = 13$), nor did we find a relationship between PC1 and male bower quality ($r_s = 0.07$, $p = 0.82$, $n = 13$). There was, however, a significant relationship between PC1 and number of bower decorations ($r_s = 0.63$, $p = 0.02$, $n = 13$), and between number of bower decorations and male mating success ($r_s = 0.73$, $p = 0.003$, $n = 13$).

Discussion

We found that the blue rather than the UV plumage chroma is correlated with male mating success in satin bowerbirds. Also, the peak in the correlation coefficients between the 20 nm spectral intervals and male mating success is confined to the blue wavelengths suggesting that UV and reflectance of other colors do not affect male mating success.

Our results show a mismatch between peak plumage reflectance and the plumage chroma that is associated with male mating success. The short-wavelength saturated reflectance of male satin bowerbird plumage appears to result from a coherent light scattering feather structure that causes reflectance to be higher at shorter wavelengths (Doucet et al. 2006). This color producing mechanism may cause the most attractive colors not to have the highest reflectance and thereby produce the observed mismatch. Alternatively, the UV reflectance peak of male plumage may have other functions not associated with mating such as reduced detection by predators with UV limited vision (Andersson 1996, Andersson 1999).

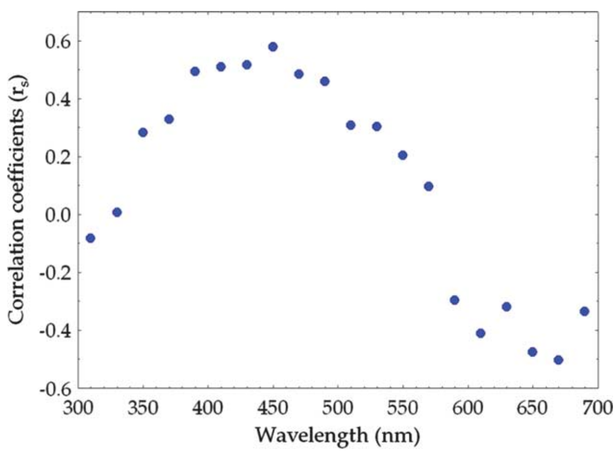

Figure 2. Spearman's rank correlation between male mating success and brightness standardized plumage reflectance for 20 nm spectral intervals.

Table 1. Comparison of factor loadings of PCs between our study and the first study of satin bowerbird plumage reflectance.

	PC1 loadings	
	this study	Doucet and Montgomerie 2003a
Total Brightness	0.18	0.70
UVV Chroma	0.97	0.39
Contrast	0.79	0.59
Hue	−0.84	loading not reported

The greater importance of blue over UV reflectance in male satin bowerbird plumage coloration is also found in male satin bowerbird decoration preferences (Borgia 2008). This is different from food color preferences (Borgia and Keagy 2006) suggesting that such preferences are not determined by tuning of the visual system. This is further supported by the lack of evidence of spectral tuning of the visual system of different species of bowerbirds that have very different decoration color preferences (Zwiers 2009, Coyle, Hart and Borgia unpubl.). The use of blue rather than UV in satin bowerbird sexual display may result, in part, from the UV poor light environment on the forest floor (Endler 1992, Gomez and Théry 2004) where satin bowerbird displays occur, which can influence the evolution of color patterns (McNaught and Owens 2002, Heindl and Winkler 2003).

Our finding of an insignificant role of UV plumage reflectance in sexual signaling differs from a previous study of satin bowerbird plumage (Doucet and Montgomerie 2003a). That study did not show an independent relationship between UV and mating success. In their plumage score (PC1), UVV chroma is the only variable directly assessing variance in UV reflectance and its low loading suggests a comparably low contribution to the PC1 score. Also, they used bower decorations and bower quality as proxies for male mating success and in satin bowerbirds these display traits account for less than half of the variation in male mating success (Borgia 1985b), so it is quite possible that their proxies for mating success did not accurately estimate values for this variable. In this study we found that only one of the two proxy variables they used showed a significant correlation with mating success. Since we found a direct relationship between blue, but not UV, chroma and a direct measure of male mating success, our results likely provide a more accurate assessment of the relationship between UV plumage color and male attractiveness in satin bowerbirds.

Our differing conclusions could be due to different reflectance patterns in the two satin bowerbird subspecies used in these studies. However, we found that the plumage reflectance spectra are qualitatively the same when museum specimens of these subspecies are compared (J-F Savard unpubl.).

In satin bowerbirds, blue is more important than UV plumage coloration in mate choice even though UV has higher reflectance. The observed mismatch between the peak reflectance of male plumage and the chroma that is correlated with mating success shows that a peak in plumage reflectance does not necessarily indicate the importance of that color in sexual signalling and that it is not safe to infer a role for UV in mate choice simply because of a relatively high UV reflectance.

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References

Andersson, M. 1994. Sexual selection. – Princeton University Press.

Andersson, S. 1996. Bright ultraviolet colouration in the Asian whistling-thrushes (*Myiophonus* spp.). – Proc. R. Soc. B 263: 843–848.

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.

Andersson, S. and Amundsen, T. 1997. Ultraviolet colour vision and ornamentation in bluethroats. – Proc. R. Soc. B 264: 1587–1591.

Andersson, S. and Prager, M. 2006. Quantifying colors. – In: Hill, G. E. and McGraw, K. J. (eds), Bird Coloration. Harvard University Press, Cambridge, pp. 589.

Andersson, S., Örnborg, J. and Andersson, M. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. – Proc. R. Soc. B 265: 445–450.

Ballentine, B. and Hill, G. E. 2003. Female mate choice in relation to structural plumage coloration in blue grosbeaks. – Condor 105: 593–598.

Bennett, A. T. D. and Cuthill, I. C. 1994. Ultraviolet vision in birds: what is its function? – Vision Res. 34: 1471–1478.

Borgia, G. 1985a. Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhynchus violaceus*). – Behav. Ecol. Sociobiol. 18: 91–100.

Borgia, G. 1985b. Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*)-an experimental analysis. – Anim. Behav. 33: 266–271.

Borgia, G. 1995. Complex male display and female choice in the spotted bowerbird: specialized functions for different bower decorations. – Anim. Behav. 49: 1291–1301.

Borgia, G. 2008. Experimental blocking of UV reflectance does not influence use of off-body display elements by satin bowerbirds. – Behav. Ecol. 19: 740–746.

Borgia, G. and Keagy, J. 2006. An inverse relationship between decoration and food colour preferences in satin bowerbirds does not support the sensory drive hypothesis. – Anim. Behav. 72: 1125–1133.

Borgia, G., Coyle, B. and Zwiers, R. B. 2007. Evolution of colorful display. – Evolution 61: 708–712.

Borgia, G., Kaatz, I. M. and Condit, R. 1987. Flower choice and bower decoration in the satin bowerbird *Ptilonorhynchus*

violaceus: a test of hypotheses for the evolution of male display. – Anim. Behav. 35: 1129–1139.
Collias, E. C., Collias, N. E., Jacobs, C. H., McAlary, F. and Fujimoto, J. T. 1979. Experimental evidence for facilitation of pair formation by bright color in weaverbirds. – Condor 81: 91–93.
Darwin, C. R. 1871. The descent of man, and selection in relation to sex. – John Murray, London.
Delhey, K., Peters, A., Biedermann, P. H. W. and Kempenaers, B. 2008. Optical properties of the uropygial gland secretion: no evidence for UV cosmetics in birds. – Naturwiss. 95: 939–946.
Diamond, J. 1986. Biology of birds of paradise and bowerbirds. – Ann. Rev. Ecol. Syst. 17: 17–37.
Doucet, S. M. and Montgomerie, R. 2003a. Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. – Behav. Ecol. 14: 503–509.
Doucet, S. M. and Montgomerie, R. 2003b. Structural plumage colour and parasites in satin bowerbirds *Ptilonorhynchus violaceus*: implications for sexual selection. – J. Avian Biol. 34: 237–242.
Doucet, S. M., Shawkey, M. D., Hill, G. E. and Montgomerie, R. 2006. Iridescent plumage in satin bowerbirds: structure, mechanisms and nanostructural predictors of individual variation in colour. – J. Exp. Biol. 209: 380–390.
Eaton, M. D. and Lanyon, S. M. 2003. The ubiquity of avian ultraviolet plumage reflectance. – Proc. R. Soc. B 270: 1721–1726.
Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. – Am. Nat. 139: S125–S153.
Endler, J. A., Westcott, D. A., Madden, J. R. and Robson, T. 2005. Animal visual systems and the evolution of color patterns: Sensory processing illuminates signal evolution. – Evolution 59: 1795–1818.
Gilliard, E. T. 1956. Bower ornamentation versus plumage characters in bower-birds. – Auk 73: 450–451.
Gilliard, E. T. 1969. Birds of paradise and bower birds. – Published for the American Museum of Natural History [by] Natural History Press, Garden City, N.Y.
Gomez, D. and Théry, M. 2004. Influence of ambient light on the evolution of colour signals: comparative analysis of a Neotropical rainforest bird community. – Ecol. Lett. 7: 279–284.
Guilford, T. and Harvey, P. H. 1998. The purple patch. – Nature 392: 867–868.
Hausmann, F., Arnold, K. E., Marshall, N. J. and Owens, I. P. F. 2003. Ultraviolet signals in birds are special. – Proc. R. Soc. B 270: 61–67.
Heindl, M. and Winkler, H. 2003. Interacting effects of ambient light and plumage color patterns in displaying wire-tailed manakins (Aves, Pipridae). – Behav. Ecol. Sociobiol. 53: 153–162.
Hunt, S., Bennett, A. T. D., Cuthill, I. C. and Griffiths, R. 1998. Blue tits are ultraviolet tits. – Proc. R. Soc. B 265: 451–255.
Hunt, S., Cuthill, I. C., Bennett, A. T. D., Church, S. C. and Partridge, J. C. 2001. Is the ultraviolet waveband a special communication channel in avian mate choice? – J. Exp. Biol. 204: 2499–2507.
Johnsgard, P. 1994. Arena Birds: Sexual Selection and Behavior. – Smithsonian Inst. Press, Washington D.C.
Kusmierski, R., Borgia, G., Crozier, R. H. and Chan, B. H. Y. 1993. Molecular Information on bowerbird phylogeny and the evolution of exaggerated male characteristics. – J. Evol. Biol. 6: 737–752.
Kusmierski, R., Borgia, G., Uy, A. and Crozier, R. H. 1997. Labile evolution of display traits in bowerbirds indicates reduced effects of phylogenetic constraint. – Proc. R. Soc. B 264: 307–313.
Liu, M., Siefferman, L. and Hill, G. E. 2007. An experimental test of female choice relative to male structural coloration in eastern bluebirds. – Behav. Ecol. Sociobiol. 61: 623–630.
Madden, J. R., Endler, J. A. and Jury, F. 2004. Morphological signals of sex and status in spotted bowerbirds. – Emu 104: 21–30.
Marshall, A. J. 1954. Bower-birds; their displays and breeding cycles, a preliminary statement. – Clarendon Press, Oxford.
McNaught, M. K. and Owens, I. P. F. 2002. Interspecific variation in plumage colour among birds: species recognition or light environment? – J. Evol. Biol. 15: 505–514.
Montgomerie, R. 2006. Analyzing Colors. – In: Hill, G. E. and McGraw, K. J. (eds), Bird coloration. Harvard University Press, Cambridge, pp. 90–147.
Morrison-Scott, T. C. S. 1937. Experiments on colour vision in the satin bower-bird (*Ptilonorhynchus violaceus*), with other observations. – Proc. Zool. Soc. A 107: 41–49.
Oakes, E. J. 1992. Lekking and the evolution of sexual dimorphism in birds: comparative approaches. – Am. Nat. 140: 665–684.
Pearn, S. M., Bennett, A. T. D. and Cuthill, I. C. 2001. Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*. – Proc. R. Soc. B 268: 2273–2279.
Reynolds, S. M., Dryer, K., Bollback, J., Uy, J. A. C., Patricelli, G. L., Robson, T., Borgia, G. and Braun, M. J. 2007. Behavioral paternity predicts genetic paternity in satin bowerbirds (*Ptilonorhynchus violaceus*), a species with a non-resource-based mating system. – Auk 124: 857–867.
Siitari, H., Alatalo, R. V., Halme, P., Buchanan, K. L. and Kilpimaa, J. 2007. Color signals in the black grouse (*Tetrao tetrix*): signal properties and their condition dependency. – Am. Nat. 169: S81–S92.
Silbergleid, R. E. 1977. Communication in the Lepidoptera. – In: Sebeok, T. A. (ed.), How animals communicate. Indiana University Press, pp. 362–402.
Stein, A. C. and Uy, J. A. C. 2006. Plumage brightness predicts male mating success in the lekking golden-collared manakin, *Manacus vitellinus*. – Behav. Ecol. 17: 41–47.
Wojcieszek, J. M., Nicholls, J. A., Marshall, N. J. and Goldizen, A. W. 2006. Theft of bower decorations among male satin bowerbirds (*Ptilonorhynchus violaceus*): why are some decorations more popular than others? – Emu 106: 175–180.
Zwiers, P. 2009. Use of molecular techniques to address the evolution of display traits in the Ptilonorhynchidae and other passeriform species. – PhD thesis, Univ. of Maryland, College Park.