*Revista Brasileira de Ornitologia 14 (3) 191-195*
*setembro de 2006*

# The role of ultraviolet wavelength in sexual selection

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*Recebido em 30 de dezembro de 2005; aceito em 30 de junho de 2006*

RESUMO. **O papel do comprimento de onda ultravioleta na seleção sexual.** Diferentemente dos seres humanos, as aves podem detectar o comprimento de onda ultravioleta. Em geral, praticamente todas as famílias de aves apresentam alguma refletância UV em sua plumagem. Entretanto, este provável canal de comunicação entre aves vinha sendo ignorado até recentemente. Esta revisão apresenta diferentes metodologias que têm sido aplicadas no estudo do papel do comprimento de onda UV na seleção sexual. Esta área de pesquisa requer a atenção ao avaliar a relação entre a reflectância UV e aspectos como: custo energético da produção da plumage estrutural, disponibilidade do recurso durante a muda, carga de parasita, presença de um dimorfismo sexual no comprimento de onda UV em diversas espécies de aves, como também sua influência na competição intra-específica. Todas estas relações devem ser avaliadas no contexto da seleção sexual.

Palavras-chave: Refletância ultravioleta, coloração estrutural, seleção sexual, escolha de parceiro.

ABSTRACT. Differently from human beings, birds can detect ultraviolet wavelengths. In general, practically all bird families present some UV reflectance in their plumage. However, this probable channel of communication between birds has been ignored until recently. This review presents different methodologies that have been applied in the study of the role of UV wavelength in sexual selection. This area of research requires attention to evaluete the relation between UV reflectance and aspects such as: energetic cost of structural plumage production, resource availability during molt, parasite load, presence of a sexual dimorphism in UV wavelength in diverse bird species, as well as its influence in intraspecific competition. All these relations must be evaluated in the context of sexual selection.

Key words: Ultraviolet reflectance, structural coloration, sexual selection, mate choice.

Much attention has been given to how individual variations in coloration could function as signals of intra- and inter-sexual interactions (Andersson 1994). However, because human vision does not detect ultraviolet wavelengths, the possibility of other animals using UV reflectance patterns to communicate has been mostly neglected.

Differently from human vision, which is trichromatic with three different single cones (Wyszecki and Stiler 1982) and a visible spectrum between 400-700 nm, the majority of birds presents tetrachromatic color vision, with four single cones (Chen *et al*. 1984, Bowmaker *et al*. 1997). This allows the detection of near-ultraviolet wavelengths (320-400 nm), which probably allows a role in sexual selection (Burkhardt 1989).

According to Eaton and Lanyon (2003) UV reflectance, in different levels, is present at least in one part of the body in birds of practically all bird families. This is not to say, however, that all birds use reflectance UV as a sexual ornament. For example, birds that live in open areas will have more chances to use reflectance UV as a signal (Eaton 2006). Parts of the plumage the bird exhibits for its partner during the display may also be an important considaration.

Ornamental coloration of the plumage can result from two different mechanisms: pigments deposited in the feathers and feather microstructures. The two most common classes of pigment are the melanins that produce colors ranging from brown to black, and the carotenoids that produce colors ranging from yellow to red. Structural coloration, on the other hand, is produced when microstructures in the reflective keratin of the feather scatter the incident light and reflect the shorter wavelengths, giving the feathers a green, blue, purple and iridescent coloration (Finger 1995). This type of microstructure is responsible for UV reflectance.

The coloration of plumage is one of the most studied characteristics of birds and probably the one most closely associated with sexual selection. However, the majority of studies were conducted upon pigment-based plumages, and not on structural plumage.

Studies that focus upon the possible effect of individual quality in the variation of UV coloration are still scarce (Keyser and Hill 2000, Doucet 2002). Nevertheless, it is probable that variations in structural coloration and their production costs must contribute, amongst other things, in determining mate choice and male-male interactions. Recent studies have shown the importance of the structural plumage to assess parasit loads and health condition (Mougeot *et al*. 2005, Hill *et al*. 2005). Thus, UV coloration could be used as an honest signal of individual quality.

Possible functions of UV colorations are sugested in the literature. Burkhardt (1989) suggested that UV reflectance could be a form of visual communication between birds during mate choice without attracting possible predators, although passerines are also preyed upon by other birds. Other studies demonstrated the importance of UV vision in foraging (european kestrels *Falco tinnunculus;* Viitala *et al*. 1995), in navigation and as a way of calibrating circadian rhythms (Tovée 1995).

In the brief review presented below, studies were grouped according to similarity of methodology.

## Cage experiments

*Apparatus used similar to Swaddle and Cuthill (1994) and Bennett et al. (1996).* The studies discussed on in this part had followed practically the same methodology. It was carried on an apparatus that consisted of a central area where the test bird was positioned and four others stimulus cages located to the end of each arm, where the stimulus birds were placed to be observed for the test bird. The test bird could look at just one stimulus bird each time.

Bennett *et al*. (1997) tested if individual variation in reflectance UV is used on mate choice decisions by forcing female starlings (*Sturnus vulgaris*) to choose between the same males under conditions in which their natural UV reflectance was either present or absent. They observed that females ranked male in the same way under the same lighting conditions, but females ranked males differently under conditions of UV presence or absence. However, it was observed that even in the absence of UV wavelength the females made consistent choices, demonstrating the importance of other characteristics in their analysis.

A study carried through with starlings and blue tits (*Parus caeruleus*) showed that neither one had a preference for a determined type of environment, with or without UV. However, female blue tits showed a strong preference for males under a full spectrum (320-700 nm), in the same way that female starlings showed a significant preference for potential males seen under conditions of UV presence (Maddocks *et al*. 2001), corroborating the previous work of Bennett *et al*. (1997).

Hunt *et al*. (1999), observed that blue tits showed a preference for partners under the presence of UV, and that this preference was more evident and statistically significant in males than in females, being considered only a tendency in females. This suggests that female choice is influenced by other criteria. Other study using the same apparatus showed that female blue tits had a strong preference for males with the brightest crests under UV (Hunt *et al*. 1998).

In blue tits, that for the human eyes it is considered monomorfic, when analysed by spectrofotometria (320-700 nm) was observed that males have a dimorfic plumage on UV waveband, suggesting that the sexual dimorfism in the coloration of this species is higher in this region of the espectrum than that of human visible wavelengths (Andersson *et al*. 1998, Hunt *et al*. 1998).

Some studies have used the zebra finch (*Taeniopygia guttata*) as a model to test the role of UV wavelength in mate choice. Bennett *et al*. (1996) showed that zebra finch females prefer males shown under the full spectrum, that is, UV and human visible wavelengths, over males which had their UV reflection removed. The study also tested choice for individuals of the same sex, which could be asocieted with flock selection. But this part of the study showed that females had a strong preference for associating with individuals of the opposite sex, demonstrating that UV light, in this species, appears to be unrelated with social flocking, but acts in a mate choice context. On the other hand, Hunt *et al*. (2001) removed sigle blocks of the visible spectrum of the experimental birds, which resulted in males without some wavelengths, including UV. There was no evidence in this study that UV was a special wavelengh in the sexual signalling of zebra finches. The red wavelength was the one that most influenced choice of females, suggesting the importance of non-UV wavelenght in sexual selection.

In a study using budgerigars (*Melopsittacus undulatus*) Pearn *et al*. (2001) observed that females spent a significantly higher time in front of males under UV lighting when compared with males exposed in its absence. Thus the results suggest that UV waveband is also used in mate choice in this species. The results of these studies as well as others not covered here clearly show that UV reflectance has an important role in the sexual signalling of birds, not restricting to flock preferences as also observed with individuals of the same sex.

*Other cage experiments*. Different types of apparatus and other methodologies have been used in other laboratory studies. Pearn *et al*. (2003) used an apparatus where there were only two arms leaving a central cage, but following the same line of Swaddle and Cuthill (1994) and Bennett *et al*. (1996), where the tested bird could only see one stimulus bird at a time. This study strengthened the argument that UV reflectance is used in the sexual signalling of budgerigars. They showed that, as observed in other studies, females did not have the same preference for males when UV wavelength was absent. This complements what was observed by Pearn *et al*. (2001), where a significant preference for males in the presence of UV wavelength was observed (Pearn *et al*. 2003).

In an experiment with bluethroats (*Luscinia s. svecica*) in an external aviary using a method based on sunblock chemicals to modify UV reflectance, a strong association by females with males who had no reduction of their UV reflectance was observed. Another interesting caracteristic demonstrated in this study was an age-related relation with UV reflectance, showing that older males presented more UV reflectance than younger males (Andersson and Amundsen 1997).

## Field studies with feathers analysis

Several studies have been conducted in the field, and involved the capture of individuals for feather collection and analysis of plumage coloration using a spectrometer. Some studies also used feather samples from individuals in museum collections (Andersson and Amundsen 1997, Bridge and Eaton 2005). Included in the following discussion are also studies where individuals were marked and had their mating and reproduction accompanied, however, without any kind of manipulation in theirs plumage characteristics.

Body-condition seems to influence the exhibition of structural coloration, thus honestly reflecting the individual quality. Studies with Sterna terns, blue-black grassquit (*Volatinia jacarina*) and blue grosbeaks (*Passerina caerulea*) have shown that structural coloration may be condition dependent and have a potential function in sexual signalling (Keyser and Hill 1999, Doucet 2002, Bridge and Eaton 2005). Differences in reproductive success and earlier arrivals at reproductive sites have also been associated with UV reflectance. In pied flycathers (*Fidecula hypoleuca*), males with higher UV reflectance on their dorsal side arrived earlier at their reproductive sites, suggesting that the relative UV reflectance on their backs must be positively associated with male quality in this species (Siitari and Huhta 2002). Also, in eastern bluebirds (*Sialia sialis*) males with more ultraviolet hues had a higher reproductive success, producing more offspring, indicating that UV reflectance may signal male quality (Siefferman and Hill 2003).

However, despite the already demonstrated importance of UV wavelength reflectance in sexual selection, other secondary sexual characters have, at least, equal importance upon the females making process decision, and it is clear that they can assess a mixture of characters simultaneously. Doucet and Montgomerie (2003a) suggested that male plumage coloration and the quality of bower characteristics are intrinsically related in satin bowerbirds (*Ptilonorhynchus violaceus*) and that, together, these elaborated sexual ornaments disclose important aspects of male quality. The study showed that female satin bowerbirds can evaluate parasite intensity through male UV plumage coloration during courtship. Doucet and Montgomerie's (2003b) findings support the predictions of the Hamilton and Zuk (1982) parasite-mediated sexual selection model.

Few studies have tried to analyze the influence of UV reflectance in intrasexual competition. In a study with blue grosbeaks (*Passerina caerulea*) it was observed that males with more elaborate structural plumage were physically larger, kept greater territories with abundant prey, and exhibited higher leves of parental care. These results indicate that UV reflectance is an honest signal of quality that can be accessed during mate choice as well as male-male competition (Keyser and Hill 2000).

### Field manipulations

Similarly to Andersson and Amundsen's (1997) experiment in captivity, Johnsen *et al*. (1998) coated the throat plumage of a group of bluethroats males with a cream that absorbs UV but leaves the human-visible reflectance (400-700 nm) unchanged. But differently from Andersson and Amundsen (1997), the treatment was applied on free-ranging males. Their results did not show a significant difference in intrasexual competition, but they observed that males with UV-reduced reflectance stayed more time together with their females to prevent extra-pair copulations. A tendency was found of UV-reduced males having more extra-pair young in their nests. UV-reduced males started to reproduce later, sang less to attract other females for extra-pair copulations, and had fewer extra-pair young in the nests of other males, when compared with the group of UV reflecting males. This study supported the results found Andersson and Amundsen's (1997) cage experiment, strengthening the idea that UV reflectance is used as a signal in mate choice for females of bluethroats in their natural environment.

Male-male competition was also exeperimentaly tested on eastern bluebirds by manipulating the number of nestboxes available. The study showed that males that fledged more offspring were more colorful on the UV espectrum than those who lost the competitions for nest sites (Siefferman and Hill 2005).

## FINAL CONSIDERATIONS

In summary, the studies included in this review show that researchers tend to focus the relation between the presence or absence of UV wavelength, and mate choice, often leaving other important aspects that must later be studied, as for example how individual variations in UV reflectance is acting in this choice or what factors could be altering this individual variations. Future researches must search to clarify the importance of detection of this "hidden" wavelength in sexual selection as in other kinds of behavior as forraging, migration, competition, among others.

The use of different methodologies in the study of UV role in sexual selection is important in such a way to corroborate the idea that this wavelength is used as a signal during the courtship and competition, as also to test other aspects related with the detection of this wavelength. However, we must be cautious to the speech that the UV is a special wavelength with a special function, not ignoring its role in sexual selection, but taking in consideration other morphological and behaviour characteristics, as also the other wavelengths and their functions during the courtship.

On this way, a vast area of research is still wide open, needing new studies concerning the cost of production of structural plumage, the availability of resource during molt and the effects on UV coloration, as also others studies about parasites load and their influence in UV reflectance. As well as studies evaluating the effects of UV reflectance on the reproductive success, extra-pair copulations; and on intraspecific competition.

## ACKNOWLEDGMENTS

I would like to thank Regina Macedo and two anonymous referees for useful comments on the paper. This research was supported by a scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES.

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