

Ultraviolet (UV) light perception by birds: a review

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ABSTRACT: The ability to perceive the near ultraviolet part of the light spectrum (the wavelength 320–400 nm) has been detected in many bird species. This ability is an important bird sense. The ecological importance of UV perception has been studied mainly in the context of intra- and inter-sexual signalling, common species communication and also in foraging. Some birds of prey use UV reflectance in their feeding strategy: e.g., the kestrel (*Falco tinnunculus*), but also other birds of prey are able to recognize the presence of voles by perceiving the UV reflectance of their scent urine marks. The ability to detect the presence of prey is a common feature of birds with analogous feeding spectra in taxonomically distinct species. UV perception and its use in foraging have also been proved in predominantly herbivorous bird species. This ability is possessed both by bird species living in northern habitats and others living in tropical forests. The signalling and communication role of the UV perception is very important. The plumage of many bird species shows specific colour features – e.g., sexually different regions in plumage coloration unnoticed by the human eye. Also other body parts can have similar features – e.g., supra-orbital combs in the red grouse (*Lagopus lagopus scoticus*). All these characteristics are important primarily in the mate-choice decision. Birds apparently also use their ability of UV perception for recognition of their own eggs. Some bird species are able to modify plumage UV reflectance by uropygial secretions. The knowledge of all specific aspects of bird physiology can significantly help both breeders of various bird species and facilitate effective veterinary care.

Keywords: UV; reflectance; food detection; coloring; plumage; communication

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1. Introduction

Sight is the dominant sense of most birds. Besides other visual particularities, the important ability to perceive UV radiation has been demonstrated in many bird species. The data available on this part of bird physiology is being increasing all the time. The basic information has already appeared in encyclopaedic publications (e.g., Veselovsky, 2001). The ability to perceive the near ultraviolet part of light spectrum (the wavelength 320–400 nm) has been indicated in a range of animal species: at least 35 diurnal bird species (obviously mainly diurnal raptors, frugivorous, nectarivorous and insectivorous species), four rodent species, 11 reptilian spe-

cies and two amphibian species (Honkavaara et al., 2002). Most of this data has been gleaned recently. Burkhardt (1996) notes that most birds have three cone types with absorption maxima in the ranges 450–480 nm, 510–540 nm, and 565–620 nm and suggests tetrachromatic colour vision. He presents some examples of the possible significance of UV perception by birds: reflection of UV from feathers as well as from fruits with waxy layers.

It is now known that avian ocular media do not absorb UV light before it reaches the retina; thus UV sensitivity in birds is possible. Birds have 4–5 types of single cone photoreceptors, including one type sensitive to UV light (for comparison humans have only three types of cone photorecep-

tors). Many birds (obviously the majority of species, e.g., many non-passerines) have a violet-sensitive single cone that is obviously sensitive to UV wavelengths. Other species (e.g., some passerines) have a single cone that has maximum sensitivity to UV light. The input of the UV cone is involved in bird chromatic colour vision system: this role of UV light in the detection of chromaticity differences (colour vision) was studied on the European starling (*Sturnus vulgaris*) as an example of Passerines, and the Japanese quail (*Coturnix japonica*) as an example of non-passerine (Order Galliformes in this case). Birds of both species distinguished between a long wave control of orange versus red stimuli and UV versus “non-UV” in the same way. They were able to discriminate spectral stimuli in accordance with the amount of the reflected light in the UV part of the spectrum composed of longer wavelengths (Veselovsky, 2001; Smith et al., 2002).

The objective of the study was also a comparison of the bird light spectrum perception with that of human. However, the differences between bird (specifically pigeon) and human vision including UV wavelengths perception has already been discussed by Cuthill and Bennett (1993); they have noted the lack of information concerning wild birds. Recently, the spectral sensitivity of domestic ducks (*Anas platyrhynchos domesticus*) and turkeys (*Meleagris gallopavo gallopavo*) was tested over a range of specified wavelengths, including UVA, between 326–694 nm in comparison with human spectral sensitivity (Barber et al., 2006). The results showed that ducks and turkeys had similar spectral sensitivities and could perceive UVA radiation. Turkeys were more sensitive to UVA than ducks. The peak sensitivity was in the wavelengths between 544–577 nm, with reduced sensitivity at 508–600 nm. Both bird species had a very different and broader range of spectral sensitivity than humans.

Some genetic aspects of the visual abilities of birds have also been studied recently. Odeen et al. (2009) reported on *in vitro* mutation studies, which allow the prediction of the maximum absorbance wavelengths (λ_{\max}) of avian UV/violet sensitive visual pigments (SWS1) from the identity of a few key amino acid residues in the opsin gene. Simply from the λ_{\max} , the absorbance spectrum of a cone's visual pigment and its pigmented oil droplet can be determined. Thus in λ_{\max} , the molecular data from genomic DNA predict the gross differences between the violet- and ultraviolet-sensitive subtypes of SWS1 opsin. It is possible to detect the en-

tire spectral sensitivity of bird species using genetic samples from live birds or museum specimens. The authors obtained partial sequences covering three of the known spectral tuning sites in the SWS1 opsin and predicted λ_{\max} for all bird species, for which the spectral absorbance has been measured by microspectrophotometry. They also proved that one bird species under examination – the bobolink *Dolichonyx oryzivorus* (Passeriformes, Icteridae) – has apparently more than one SWS1 visual pigment in its retina.

The ecological importance of UV vision has mainly been studied in the context of intra- and inter-sexual signalling, species signalling and also in foraging (Veselovsky, 2001; Honkavaara et al., 2002); UV vision is also important in navigation, wide intraspecies communication and the control of circadian rhythms, and all this in different taxons, including both vertebrates and invertebrates (Tovee, 1995).

An understanding of all specific aspects of bird physiology can significantly help both breeders of various bird species (e.g., in breeding of endangered bird species, poultry) and improve veterinary care.

2. Prey detection in birds of prey

Quite a lot is known about the ability of birds of prey to perceive UV radiation. Some species are known to use UV reflectance in their food strategy. Foraging birds may use either UV cues (reflectance or absorbance) of food items or UV cues of the environment. This ability was experimentally studied in the common kestrel (*Falco tinnunculus*). Kestrels are able to recognize vole trails (mainly *Microtus arvalis*, *Microtus agrestis* and other usual prey) by perceiving the UV reflectance of scent marks. These marks from vole urine appear in UV radiation as yellow. The question of whether the use of scent marks in the UV range is an innate feature or if it is acquired by experience was tested by Zampiga et al. (2006) in experiments on adult and juvenile individuals. The authors deduced that the association between vole scent UV reflectance and the presence of voles is an innate component, but that the ability to detect UV cues is a learned component. The ability to use UV reflectance in food strategy has been demonstrated not only in birds of prey (birds of order Falconiformes), but also in carnivorous birds of other orders, e.g., order Passeriformes. The results of experiments on the

great grey shrike (*Lanius excubitor*) indicate that this passerine probably uses UV cues to determine the presence of voles (Probst et al., 2002). However, the ability to detect prey is common for birds with analogous feeding spectra in taxonomically distinct species. In many areas, there are fluctuations in small rodent (mainly voles) populations between years (usually over a four-year period). Viitala et al. (1995) examined the reaction of common kestrels (*Falco tinnunculus*) to small rodent population density in northern Europe. The results of laboratory and field experiments on the common kestrel and the vole *Microtus agrestis* explain how raptors detect patches of high vole density without prior knowledge of rodent quantity as a food resource. Kestrels flying over landscape follow the vole marks – urine and faeces – that are visible in the UV light in order to assess the numbers of prey. The ability to follow these marks of the presence of voles enables the raptors to screen large areas in a relatively short time.

The same ability was demonstrated for the rough-legged buzzard (*Buteo lagopus*) (Koivula and Viitala, 1999). During field experiments in northern Finland, these buzzards were observed more often in localities with vole marks. It is evident that they use these marks in choosing the prey hunting and breeding area.

3. Food detection by other birds

UV perception and its importance in foraging have also been studied in predominantly herbivorous bird species. A possible UV sensitivity of the black grouse (*Tetrao tetrix* – Order Galliformes, Family Tetraonidae) is indicated by the results of laboratory experiments on these birds. Black grouses preferred UV-reflecting bilberries (*Vaccinium myrtillus*) to two colour morphs of bilberry (UV-reflecting and non-UV-reflecting); no preferences were observed in the absence of the UV light (Siitari and Viitala, 2002). The above observation was made in northern habitats (e.g., tundra and taiga). It is consistent that similar strategies occur in habitats with maximally wide biodiversity – tropical rainforests.

The significant role of UV reflectance in relations between plants and frugivores was demonstrated by Altshuler (2001), who tested the reflectance spectra of fruits from 57 tropical plant species on Barro Colorado Island in Panama. UV-reflecting fruits were present in both open and closed light habitats and were strongly associated with the occurrence of

birds and rodents, both of which perceive UV radiation. A key fact is that only mature fruits reflected the UV – it is a visual signal for frugivore birds or other frugivores. The understory shrub *Psychotria emetica* (Family Rubiaceae) was chosen as an example for an experimental study on the removal of fruit. During a 3-month period, the ambient light was manipulated by placing a UV-absorbing filter over fruiting plants, with control treatments of plants under clear filters (UV-transmitting) and plants without filters. Fewer fruits were removed from shrubs under the UV-absorbing filter, showing that UV reflectance can be an important attractant for the consumption of some fruit (and dispersal of its seed). This study establishes a relationship between the perceptual abilities of animals (including frugivorous birds as an example of animals finding their food by visual sense) and the colour of the fruits they consume.

Experiments have also been carried out on free-flying crows (*Corvus ossifragus*) under the seminatural conditions in an aviary. The important result of these experiments was that the discrimination of coloured objects (e.g., fruits) by birds can be influenced by the background. Thus, experiments on colour perception can be improved by incorporating background-specific effects (Schaefer et al., 2006). The experimental crows detected red fruits at a larger distance than black fruits. Artificial red fruits had higher chromatic and lower achromatic contrasts against foliage than artificial black fruits, so the crows apparently prioritized chromatic contrast. The colour change in the fruit colour from red to black during ripening thus does not increase attractiveness to the crows. The crows were also tested against two types of black berries (*Vaccinium myrtillus*): UV-reflecting berries and black blueberries, against backgrounds of foliage and against backgrounds of sand. In the first case – against foliage – the crows detected the UV-reflecting berries at a larger distance, because these fruits had higher chromatic and achromatic contrasts. Against the backgrounds of sand, the UV-reflecting berries had low achromatic contrasts and black berries had low chromatic contrasts. As the crows detected both black berry types equally, they apparently used chromatic contrasts to detect the UV-reflecting berries, and the achromatic contrasts to detect the black berries.

Other studies have been carried out in the frequent bird model, the zebra finch (*Taeniopygia guttata* – Order Passeriformes, Family Estrildidae). The removal of UV wavelengths significantly changed

the strength and frequency dependence of the seed preferences compared to the full-spectrum illumination. It did not affect the strength of frequency dependence compared to the removal of the short wavelengths (approximately 400–500 nm), medium wavelengths (approximately 500–600 nm) or long wavelengths (approximately 600–700 nm; Church et al., 2001). The authors discuss the possibility of ecological impact: the affect on the dynamics of the plant population depending upon the spectral quality of ambient light (it differs considerably depending on the climate, time of the day and local habitat geometry), but they warn of overestimating the importance of UV light compared to the human-visible spectrum.

Insectivorous birds also use chromatic cues in the search for prey. The principal for the finding of food is the differentiation of food in its background. Blue tits (*Cyanistes caeruleus*) were presented with two prey types that were achromatically identical but different in their chromatic properties in the UV/blue range on two achromatically identical backgrounds. The backgrounds had either the same chromatic properties as the prey (matching combination) or differed in their chromatic properties (mismatching combination). The tits used the chromatic cues successfully in their search in the mismatching background. The duration of prey search on the matching background was significantly longer, but the search for more chromatic prey on the same background was easier. The birds evidently used the combination of achromatic and chromatic cues for the successful search for prey (Stobbe et al., 2009).

4. Signal and communication significance

The presence of UV reflecting plumage assumes the perception of UV wavelengths and suggests ecological significance (in inter- or intra-specific relations). Muellen and Pohland (2008) describe the results of the study on the existence of plumage regions with high proportions of the UV-reflecting feathers in nine hundred and sixty-eight bird species, covering all orders. Across nine orders: Struthioniformes, Tinamiformes, Craciformes, Turniciformes, Galbuliformes, Upupiformes, Coliiformes, Apodiformes and Musophagiformes all species were tested. High proportions of UV-reflecting plumage were found in some coloured plumage regions. The species of some orders used

mostly the UV maxima between 380–399 nm, these probably have a violet sensitive (VS) cone; other orders with ultraviolet sensitive (UVS) cones had their UV maxima mostly between 300 and 379 nm.

This suggests that it is not objective to classify the colouring of the bird plumage only according to human colour perception. Conspecific can perceive the plumage colouring differently, because most birds are visually sensitive to the wavelengths in the near-ultraviolet (300–400 nm). One example is the blue tit (*Parus caeruleus* = *Cyanistes caeruleus*), whose plumage shows considerable reflection of UV light. This species is sexually dichromatic for multiple regions of the plumage such as the crest, which shows the peak reflectance at wavelengths around 352 nm. This fact is important for the mate choice: the results of the experiments indicate that the blue tit females prefer the males with the brightest crests (Hunt et al., 1998). It is possible to markedly reduce the plumage brightness in the blue tit by experimentally accelerating the moult speed on the UV/blue crown feathers (for comparison the structural white on the cheek feather was not affected). UV/Blue colours are considered as a marker of an individual's performance during the previous breeding season. The relationship between the fast moulting and the colour expression present a selective advantage for early-breeding birds (Griggio et al., 2009).

In the example of the great tit (*Parus major* – Order Passeriformes, Family Paridae), the differences in the spectral reflectance of the yellow breast feathers in yearlings (though not older birds) between some populations have been identified. These differences in coloration among young birds of different origins correspond to genetic differences that were determined earlier. Systematic differences in colour signals probably exist across populations, among individuals of different origins (Postma and Gienapp, 2009).

Also starlings (*Sturnus vulgaris* – Passeriformes, Sturnidae) have sexually different body regions in plumage coloration unnoticed by the human eye. Cuthill et al. (1999) used multivariate analyses on principal components of reflectance spectra (300 to 720 nm) of plumage samples from different body regions of male and female starlings. Sex differences occurred in some body regions (though not in all), and were more pronounced at some wavelengths (both ultraviolet and human visible).

This phenomenon occurs across the taxonomical groups; Mahler and Kempnaers (2002) found

differences in the UV reflectance of the plumage between males and females of the bird of Order Columbiformes, Family Columbidae – picui dove (*Columbina picui*). The male plumage was brighter than the one of females. Several body regions showed a significant sex difference in spectral shape, although this bird species was considered sexually monochromatic.

An interesting finding was that visible sexual dichromatism in the plumage coloration (blue males and green females) in many species of tanagers (Passeriformes, Thraupidae) is that reflectance spectrophotometry is uniform, without sexual differences. This phenomenon was investigated in the swallow tanager (*Tersina viridis*) and the blue dacnis (*Dacnis cayana*) (Barreira et al., 2008). However, males showed a secondary peak of reflectance in the UV part of the spectrum, which females do not have. This male plumage bimodal reflectance causes the visual aspect, but it is different from the common unimodal pattern of the blue plumage. In this domain, the role of the UV light perception in the communication during the avian mate choice – as one of several possibilities – was studied. Bennett et al. (1996) published the basic finding of the use of the UV light in the mate-choice decision in the zebra finch (*Taeniopygia guttata*).

In the experiments performed by Hunt et al. (2001), the female zebra finches remarkably preferred the UV-reflecting males to the males whose UV reflection was removed. In these experiments, colored filters which removed single blocks of the avian visible spectrum were used. The block filters were chosen in order to correspond with the spectral sensitivities of the single cone classes of the studied birds. Some experimental males had no UV plumage reflection; others had no short-wave (SW), no medium-wave (MW) or no long-wave (LW). The females preferred the male individuals with UV and SW. The results show that the role of the UV waveband is important in the zebra finch mate choice in conjunction with other parts of the avian visible spectrum. The reflection from different plumage areas varies. Little or no UV reflection exists in some plumage areas, but despite this fact the observed effect is very strong. However, the authors conclude that the importance of UV light compared to the other regions of the bird-visible spectrum is not clear.

A very interesting finding is that the birds appearing in the human visible light as “black and white” – penguins (two species: gentoo penguin – *Pygoscelis*

papua and king penguin – *Aptenodytes patagonicus*; Order Sphenisciformes, Family Spheniscidae) have some UV reflecting marks (Meyer-Rochow and Shimoyama, 2008). Photographs of these bird species through a filter that transmits only UV radiation and blocks all visible light reveal that king penguins with white (but not yellow or orange) auricular patches reflect UV from these areas. Also the beaks of juvenile (not adult) gentoo penguins are UV-reflecting. The authors consider this to be an “associative phenomenon” without behavioural significance. The intensive reflectance of the beak horn of the king penguin (*Aptenodytes patagonicus*) has already been described by Dresp and Langley (2006) and it is believed to have significance relating to mate choice. Both the structure of crystal-like photonic elements capable of reflecting in the near-UV and the detailed fine structure of the king penguin beak horn have also been described. The authors present the important finding that the lattice dimensions of the photonic crystals and morphological composition properties permit predictions of the wavelength of reflected light. The way of the UV signal is optimized by the fine structure of the beak tissue. There is apparently one-dimensional structural periodicity within this tissue.

An example of a bird that has plumage sexual dichromatism – invisible for humans – is the yellow-breasted chat (*Icteria virens* – Order Passeriformes, Family Parulidae; Mays et al., 2004). This species lives in Northern America, from the southern plains of Canada to central Mexico during the summer, and migrate mainly to Mexico and Central America, although some of them may spend the winter in coastal areas. Spectrophotometric analyses reveals that the plumage on this species’ neck and breast exhibits reflective curves with two peaks, one in the ultraviolet and the other at the yellow end of the spectrum. Male plumage of the breast patch reflected more UV light and yellow wavelengths than female plumage in the same part of the body. Male neck feathers appeared brighter than those of females only in the UV. The reason for this are the different concentrations of carotenoid all-trans lutein in male plumage compared to the female one. Naturally, unpigmented feathers reflected more UV light than yellow ones. This phenomenon probably has basic importance in intraspecific relations, primarily in the mate choice.

The markedly positive relationship among colour patches, brightness of plumage, male age and the mass of the offspring was described for the *Sialia mexicana*

(Passeriformes, Turdidae) by Budden and Dickinson (2009). The birds' condition and sexual preferences relate to this relationship. Some traits (plumage patch on the back, size of the rufous breast patch) show dependence on condition and/or age, while spectral characters from the wings and rump were not associated with any of the measured reproductive parameters. The results underline the importance of experimental tests to understand the mate choice in this species (naturally also for other species).

Males of congeneric species (from the same genus) – *Sialia currucoides* – have brilliant UV-blue plumage. Males of this monogamous species with brighter and more UV-blue plumage sired at least one extra pair of offspring, on average. Thus, these males were more successful at reproduction, fertilized the eggs of more females, sired more offspring both with their own mate and tended to sire offspring with extra-pair mates. The grade of the plumage colouration is evidently an important factor in sexual choice (Balenger et al., 2009).

Some bird species are able to modify the plumage UV reflectance by uropygial secretions. Two main types of uropygial secretions which reduce the relative UV reflectance of the white background exist. One type occurs predominantly in passerines, the other one in non-passerines. Secretions reduce for example the brightness and the UV reflectance of the white feathers of the mallard (*Anas platyrhynchos*) and significantly affect the reflectance of the UV/blue crown feathers of the blue tit (*Cyanistes caeruleus*). Uropygial secretions probably do not play the major role in modifying the UV reflectance of plumage, but they can be involved – in some measure – in the visual signalling system of birds (Delhey et al., 2008).

A very interesting finding is that the relationship between androgen concentrations in avian eggs and male attractiveness may exist. In experiments on blue tits (*Cyanistes caeruleus*) it was shown that the attractiveness of the males of this species lies in the UV coloration of the crown feather and it is presumed that the females are able to perceive this feature. The sexually selected UV coloration of the male crown feathers was manipulated (reduced). Levels of testosterone (not androstenedione), in eggs five and seven were higher for females with attractive males compared to those with unattractive (UV-reduced) males. The difference was not found in the ninth egg, coinciding with the recovery of the UV coloration after manipulation (similarly androgen concentrations in the second egg did not correlate with still unaffected male crown plumage).

These results suggest that females are capable of modifying testosterone content in response to changes in the sexual attractiveness of their mates (Kingma et al., 2009).

The melanin layer in the feather barbules plays the principal role in light reflectance. This layer may in some barbules be thin enough to allow interaction with the underlying keratin. The resultant plumage colour is caused by layers in the structure of the matter with different refractive indexes (in feathers keratin, melanin and air usually). This question was studied by spectrometry, electron microscopy and thin-film optical modelling with the aim of describing the UV-reflecting iridescent colour of feather barbules. For the experiments, the feather of the male blue-black grassquits – *Volatinia jacarina* (Order Passeriformes, Family Emberizidae) characterized by a keratin layer overlying a single melanin layer was used. The results indicate that both the keratin and the melanin layers are essential for production of the observed colour (Maia et al., 2009).

Another body part, in which UV reflectance was demonstrated, is the supra-orbital combs of the red grouse *Lagopus lagopus scoticus* (Galliformes, Tetraonidae). Also in this case this property acts as a signal in the mate choice, but by an unexpected mechanism. The combs reflect both the red (600–700 nm) and the UV (300–400 nm) part of the spectrum. Although the males have bigger and redder combs than females, female combs have greater UV brightness; similarly, both young males and females show brighter UV than old individuals (Mougeot et al., 2005). These authors tested also the potential influence of health in the example of parasitic invasion: the intensity of caecal threadworm *Trichostrongylus tenuis* (Nematoda) invasion was not significantly related to the comb size or brightness, but it was possible to predict the presence of fewer worms from the UV in the combs of both sexes. Thus, the UV reflectance of combs is one of the indications of the potential mate's health and can play an important role in the mate choice of this bird species.

The combs of these birds represent bright carotenoid-dependent orange-red sexual ornaments. The UV reflectance of combs decreases with increasing comb size and red colouring. The UV reflectance is a property of the dermis, underneath the epidermis. In the red pigmented epidermis, there are carotenoid pigments that reduce the reflectance of the dermis in the range 400–550 nm and in the UV, 300–400 nm. The experimental removal of the red epidermis of combs increased the UV reflectance. Patagium skin

under the grouse wings also reflects the UV, but in this body part the mediator of this property is epidermis: its removal from this bare part tends to reduce the UV reflectance (Mougeot et al., 2007).

The UV perception has also its function in the parental care of birds. A markedly coloured mouth (and surroundings) in the nestlings of many bird species are known as visual signals for their parents. Hunt et al. (2003) proved that both mouths and their surrounding flanges show two striking peaks of reflectance in the UV light, coupled with the high long-wavelength reflectance. The above mentioned high UV reflectance is apparently an important cue for the parents bringing food to nestlings, as the contrast with the nest background is maximal in the UV radiation.

Aviles and Soler (2009) compared the nestling colouration and the concurrently visual sensitivity in 22 altricial bird species and assessed some differences in performance of typical UV-tuned and violet-tuned bird eyes when looking at the nestling traits under the ordinary light regimes in their nests. The results indicate an evidently higher importance of the UV over the violet at detecting gape and body skin traits in either open- or hole-nest light conditions. Gape colouration corresponds to the visual system tuning of adult conspecific birds.

Carotenoids reduce the reflectance of ultraviolet wavelengths of the rictal flanges. Thorogood et al. (2008) carried out field experiments on *Notiomystis cincta* (Passeriformes, Noctiomystidae), with supplements of carotenoids to the nestlings and their provisioning parents. The effect on nestling mouth colouration was measured with a spectrometer. Increased carotenoid availability in the diet enhanced the circulating blood plasma carotenoid concentrations, and this influenced mouth palate and rictal flange colouration. The high carotenoid availability also increased the saturation of the yellow wavelengths of the spectrum reflected by both the palate and the flanges. Thus, carotenoids apparently influence the appearance of nestling gapes both by increasing the pigmentation and as a filter of the UV-reflecting structures and they contribute in this way to the communication between the nestlings and their parents.

UV reflectance marks occur not only in the plumage, bill and other parts of a bird's body. Birds apparently use their ability of UV perception also for recognition of their eggs. The results of experiments with recognition of variously coloured eggs (blue model eggs as mimetic, others coloured as nonmimetic eggs) by the song thrush (*Turdus phi-*

lomelos – Passeriformes, Turdidae) suggest that the decisive factors in the recognition of eggs are the UV and green parts of spectrum. These colours significantly influenced the egg rejection in this bird species (Honza et al., 2007). The significance of this property lies apparently in the recognition and rejection of the eggs of breeding parasitic birds.

5. Practical impacts on breeding, including veterinary care

A lot is evident from the above text. It is known that ultraviolet wavelengths are a component of normal avian colour perception. It is possible to expect other physiological influences of this environmental factor. Many artificial light conditions do not represent a full light spectrum. Maddocks et al. (2001) investigated the influence of the chronic long-term effects of the absence of UV light on domestic chicks (*Gallus gallus domesticus*) in connection with the welfare of these animals. The topic of the investigation was the hormonal stress response to the absence of UV light. Chicks kept in a UV light-deficient environment had significantly higher basal plasma corticosterone concentrations. The control group – chicks subjected to the full light spectrum had a significantly higher rate of corticosterone rise in stress situations compared to the chicks kept in UV light-deficient conditions, but there were some subsidiary influences (e.g., age).

Analogous results were reached by Maddocks et al. (2002) in experiments on European starlings (*Sturnus vulgaris*). Juvenile starlings had significantly higher basal plasma corticosterone concentrations in the UV-deficient light environments than those kept under the full spectrum lighting. The birds under the UV-deficient conditions showed significant changes in their behaviour (escaping behaviour). When the interval between the transfer from the wild to the experimental conditions was short (two days) birds showed significantly higher basal and maximum plasma corticosterone concentrations than starlings which were transferred after 7–14 days in captivity. In the second case, the capture stress had already subsided. Thus, the stress effects of UV light deficiency are apparently small relative to the overall impact of captivity; nevertheless, the former may become the more significant factor after the initial effects of capture subside. The authors note the significance of the full light spectrum for the welfare of captive birds.

For the study of museum specimens, it is very important to know the durability of the plumage features. Ultraviolet colour may be more susceptible to degradation than colours visible by the human eye as suggested by a study which performed measurements on five species of passerines collected over the past 100 years with a reflectance spectrophotometer. Contrary to these results, the results of the tests on the specimens collected within the past 50 years suggest that the colours were relatively unimpaired and that UV is not affected by fading more severely than human-visible colours (Armenta et al., 2008).

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REFERENCES

- Altshuler D.L. (2001): Ultraviolet reflectance in fruits, ambient light composition and fruit removal in a tropical forest. *Evolutionary Ecology Research*, 3, 767–778.
- Armenta J.K., Dunn P.O., Whittingham L.A. (2008): Effects of specimen age on plumage color. *AUK*, 125, 803–808.
- Aviles J.M., Soler J.J. (2009): Nestling colouration is adjusted to parent visual performance in altricial birds. *Journal of Evolutionary Biology*, 22, 376–386.
- Balenger S., Johnson L., Masters B. (2009): Sexual selection in a socially monogamous bird: male color predicts paternity success in the mountain bluebird, *Sialia currucoides*. *Behavioral Ecology and Sociobiology*, 63, 403–411.
- Barber C.L., Prescott N.B., Jarvis J.R., LeSueur C., Perry G.C., Wathes C.M. (2006): Comparative study of the photopic spectral sensitivity of domestic ducks (*Anas platyrhynchos domesticus*), turkeys (*Meleagris gallopavo gallopavo*) and humans. *British Poultry Science*, 47, 365–374.
- Barreira A.S., Garcia G., Lijtmaer D.A., Loughheed S.C., Tubaro P.L. (2008): Blue males and green females: Sexual dichromatism in the Blue dacnis (*Dacnis cayana*) and the Swallow tanager (*Tersina viridis*). *Ornithologia Neotropica*, 19, 441–450.
- Bennett A.T.D., Cuthill I.C., Partridge J.C., Maier E.J. (1996): Ultraviolet vision and mate choice in zebra finches. *Nature*, 380, 433–435.
- Budden A.E., Dickinson J.L. (2009): Signals of quality and age: the information content of multiple plumage ornaments in male western bluebirds *Sialia mexicana*. *Journal of Avian Biology*, 40, 18–27.
- Burkhardt D. (1996): Ultraviolet perception by bird eyes and some implications. *Naturwissenschaften*, 83, 492–497.
- Church S.C., Merrison A.S.L., Chamberlain T.M.M. (2001): Avian ultraviolet vision and frequency-dependent seed preferences. *Journal of Experimental Biology*, 204, 2491–2498.
- Cuthill I.C., Bennett A.T.D. (1993): Mimicry and the eye of the beholder. *Proceedings of the Royal Society of London, series B-Biological Sciences*, 253, 203–204.
- Cuthill I.C., Bennett A.T.D., Partridge J.C., Maier E.J. (1999): Plumage reflectance and the objective assessment of avian sexual dichromatism. *American Naturalist*, 153, 183–200.
- Delhey K., Peters A., Biedermann P.H.W., Kempenaers B. (2008): Optical properties of the uropygial gland secretion: no evidence for UV cosmetics in birds. *Naturwissenschaften*, 95, 939–946.
- Dresp B., Langley K. (2006): Fine structural dependence of ultraviolet reflections in the King Penguin beak horn. *Anatomical Record, part A-Discoveries in Molecular Cellular and Evolutionary Biology*, 288A, 213–222.
- Griggio M., Serra L., Licheri D., Campomori C., Pilastro A. (2009): Moulting speed affects structural feather ornaments in the blue tit. *Journal of Evolutionary Biology*, 22, 782–792.
- Honkavaara J., Koivula M., Korpimäki E., Siitari H., Viitala J. (2002): Ultraviolet vision and foraging in terrestrial vertebrates. *Oikos*, 98, 505–511.
- Honza M., Polacikova L., Prochazka P. (2007): Ultraviolet and green parts of the colour spectrum affect egg rejection in the song thrush (*Turdus philomelos*). *Biological Journal of the Linnean Society*, 92, 269–276.
- Hunt S., Bennett A.T.D., Cuthill I.C., Griffiths R. (1998): Blue tits are ultraviolet tits. *Proceedings of the Royal Society of London, series B-Biological Sciences*, 265, 451–455.
- Hunt S., Cuthill I.C., Bennett A.T.D., Church S.C., Partridge J.C. (2001): Is the ultraviolet waveband a special communication channel in avian mate choice? *Journal of Experimental Biology*, 204, 2499–2507.
- Hunt S., Kilner R.M., Langmore N.E., Bennett A.T.D. (2003): Conspicuous, ultraviolet-rich mouth colours in begging chicks. *Proceedings of the Royal Society of London, series B-Biological Sciences*, 270, S25–S28.
- Kingma S.A., Komdeur J., Vedder O., von Engelhardt N., Korsten P., Groothuis T.G.G. (2009): Manipulation of male attractiveness induces rapid changes in avian maternal yolk androgen deposition. *Behavioral Ecology*, 20, 172–179.

- Koivula M., Viitala J. (1999): Rough-legged Buzzards use vole scent marks to assess hunting areas. *Journal of Avian Biology*, 30, 329–332.
- Maddocks S.A., Cuthill I.C., Goldsmith A.R., Sherwin C.M. (2001): Behavioural and physiological effects of absence of ultraviolet wavelengths for domestic chicks. *Animal Behaviour*, 62, 1013–1019.
- Maddocks S.A., Goldsmith A.R., Cuthill I.C. (2002): Behavioural and physiological effects of absence of ultraviolet wavelengths on European starlings *Sturnus vulgaris*. *Journal of Avian Biology*, 33, 103–106.
- Mahler B.A., Kempenaers B. (2002): Objective assessment of sexual plumage dichromatism in the Picui dove. *Condor*, 104, 248–254.
- Maia R., Caetano J.V.O., Bao S.N., Macedo R.H. (2009): Iridescent structural colour production in male blue-black grassquit feather barbules: the role of keratin and melanin. *Journal of the Royal Society Interface*, 6, S203–S211.
- Mays H.L., McGraw K.J., Ritchison G., Cooper S., Rush V., Parker R.S. (2004): Sexual dichromatism in the yellow-breasted chat *Icteria virens*: spectrophotometric analysis and biochemical basis. *Journal of Avian Biology*, 35, 125–134.
- Meyer-Rochow V.B., Shimoyama A. (2008): UV-reflecting and absorbing body regions in gentoo and king penguin: Can they really be used by the penguins as signals for conspecific recognition? *Polar Biology*, 31, 557–560.
- 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. *Journal of Avian Biology*, 36, 203–209.
- Mougeot F., Martinez-Padilla J., Perez-Rodriguez L., Bortolotti G.R. (2007): Carotenoid-based colouration and ultraviolet reflectance of the sexual ornaments of grouse. *Behavioral Ecology and Sociobiology*, 61, 741–751.
- Mueller P., Pohland G. (2008): Studies on UV reflection in feathers of some 1000 bird species: are UV peaks in feathers correlated with violet-sensitive and ultraviolet-sensitive cones? *Ibis*, 150, 59–68.
- Odeen A., Hart N.S., Hastad O. (2009): Assessing the use of genomic DNA as a predictor of the maximum absorbance wavelength of avian SWS1 opsin visual pigments. *Journal of Comparative Physiology A-Neuroethology Sensory Neural and Behavioral Physiology*, 195, 167–173.
- Postma E., Gienapp P. (2009): Origin-related differences in plumage coloration within an island population of great tits (*Parus major*). *Canadian Journal of Zoology- Revue Canadienne de zoologie*, 87, 1–7.
- Probst R., Pavlicev M., Viitala J. (2002): UV reflecting vole scent marks attract a passerine, the great grey shrike *Lanius excubitor*. *Journal of Avian Biology*, 33, 437–440.
- Schaefer H.M., Levey D.J., Schaefer V., Avery M.L. (2006): The role of chromatic and achromatic signals for fruit detection by birds. *Behavioral Ecology*, 17, 784–789.
- Siitari H., Viitala J. (2002): Behavioural evidence for ultraviolet vision in a tetraonid species foraging experiment with black grouse *Tetrao tetrix*. *Journal of Avian Biology*, 33, 199–202.
- Smith E.L., Greenwood V.J., Bennett A.T.D. (2002): Ultraviolet colour perception in European starlings and Japanese quail. *Journal of Experimental Biology*, 205, 3299–3306.
- Stobbe N., Dimitrova M., Merilaita S., Schaefer H.M. (2009): Chromaticity in the UV/blue range facilitates the search for achromatically background-matching prey in birds. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 364, 511–517.
- Thorogood R., Kilner R.M., Karadas E., Ewen J.G. (2008): Spectral mouth colour of nestlings changes with carotenoid availability. *Functional Ecology*, 22, 1044–1051.
- Tovee M.J. (1995): Ultra-violet photoreceptors in the animal kingdom – their distribution and function. *Trends in Ecology & Evolution*, 10, 455–460.
- Veselovsky Z. (2001): General Ornithology (in Czech). Academia, Prague. 357 pp.
- Viitala J., Korpimäki E., Palokangas P., Koivula M. (1995): Attraction of Kestrels to vole scent marks visible in ultraviolet-light. *Nature*, 373, 425–427.
- Zampiga E., Gaibani G., Csermely D., Frey H., Hoi H. (2006): Innate and learned aspects of vole urine UV-reflectance use in the hunting behaviour of the common kestrel *Falco tinnunculus*. *Journal of Avian Biology*, 37, 318–322.

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