

Ultraviolet vision and foraging in terrestrial vertebrates

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Tetrachromatic colour vision, based on four ‘main’ colours and their combinations, is probably the original colour vision in terrestrial vertebrates. In addition to human visible waveband of light (400–700 nm) and three main colours, it also includes the near ultraviolet part of light spectrum (320–400 nm). The ecological importance of ultraviolet (UV) vision in animals has mainly been studied in the context of intra- and inter-sexual signalling, but recently the importance of UV vision in foraging has received more attention. Foraging animals may use either UV cues (reflectance or absorbance) of food items or UV cues of the environment. So far, all diurnal birds studied (at least 35 species), some rodents (4 species), many reptilians (11 species) and amphibians (2 species) are likely able to see near UV light. This probably allows e.g. diurnal raptors as well as frugivorous, nectarivorous and insectivorous birds to use foraging cues invisible to humans. The possible role of UV cues and existing light conditions should be taken into account when food selection of vertebrate animals is studied, particularly, in experiments with artificial food items.

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In the early 1970s, Huth and Burkhardt (1972), Wright (1972), and Diez (1972) showed that some birds and a toad could see ultraviolet (later UV) light. Since then a growing body of evidence has accumulated on UV vision of birds and other vertebrates (Goldsmith 1990, Jacobs 1992, Bennett and Cuthill 1994, Tovee 1995, Cuthill et al. 2000a). Tetrachromatic colour vision, including the UV part of light spectrum, is suggested to be the original type of colour vision in terrestrial vertebrates (Robinson 1994). So far, all diurnal birds (at least 35 species) and many reptiles and amphibians studied seem to possess tetrachromatic colour vision (Fleishman et al. 1993, Harosi 1994, Loew 1994, Deutschlander and Phillips 1995, Ellingson et al. 1995, Loew et al. 1996, Cuthill et al. 2000a). This means that the retina of eye contains at least four cone types, each having a sensitivity peak at different wavelength areas (i.e. ultraviolet, blue, green and red). Moreover, tetrachromatic colour vision in terrestrial vertebrates also includes oil droplets connected to cone cells. These oil

droplets filter the light in certain wavelengths, which, by increasing colour saturation, will enhance colour discrimination and colour constancy (Bowmaker 1980, Jane and Bowmaker 1988, Vorobyev et al. 1998). The eye of an UV sensitive vertebrate is typically sensitive to wavelengths from 320 to 700 nm as compared to the human visual spectrum from 400 to 700 nm (Tovee 1995). In fact, Maier (1993) has suggested a passerine eye may be five times more sensitive to UV than to visible light. Moreover, humans have only three types of cones (blue, green and red) and most of the mammals just two (blue and green). UV vision seems to be absent in most mammalian species, although some rodents have UV sensitive receptors (Jacobs et al. 1991, Szél et al. 1992, Jacobs and Deegan II 1994). Therefore, colour determination based on human vision is not applicable to UV sensitive study objects (Bennett and Cuthill 1994, Bennett et al. 1994).

UV vision may be used for various purposes. First, some researchers have suggested that birds may use UV

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for orientation and navigation (Kreithen and Eisner 1978, Burkhardt 1982, Schmidt-Koenig 1990, Jacobs 1992, Phillips and Moore 1992, Able and Able 1993, Wiltshko et al. 1993, Munro and Wiltshko 1995). In addition to polarization patterns and spectral gradients, the Earth's magnetic field also provides a source of information, and the short wavelengths of light may be crucial for one mechanism of the magnetoreception (Phillips and Borland 1992, Wiltshko et al. 1993, Deutschlander et al. 1999).

Second, many birds and at least some lizards have secondary sexual characters that reflect in both visible and UV spectrum (Peiponen 1963, Burkhardt 1982, 1989, Alberts 1989, Fleishman et al. 1993, Andersson and Amundsen 1997, Andersson et al. 1998, Hunt et al. 1998, LeBas and Marshall 2000). Several studies in both the laboratory and field suggest that UV wavelengths are used in mate choice and social signalling (Alberts 1989, Fleishman et al. 1993, Maier 1993, Finger and Burkhardt 1994, Bennett et al. 1996, 1997, Andersson and Amundsen 1997, Andersson et al. 1998, Johnsen et al. 1998, Hunt et al. 1997, 1998, 1999, LeBas and Marshall 2000, Siitari et al. 2002a).

Third, Burkhardt (1982) found that petals of some flowers and some fruits and berries covered by waxy bloom reflect UV light and suggested that this might affect the foraging behaviour of birds. As many natural backgrounds (e.g. leaves, bark, and soil) do not reflect UV (Endler 1993, Finger and Burkhardt 1994), the contrast between the food item and its background will increase. Recently new evidence on the importance of UV vision in foraging has accumulated and this article aims to review these studies.

Fruit-frugivore interactions

One main function of the colour of fleshy fruits is to advertise fruits to the potential seed dispersers. Most of the fruits consumed by birds in temperate zones appear to be red and/or black (Wilson and Whelan 1989), although in northern boreal areas the proportion of blue fruits is also high. Many blue berries have a waxy bloom that reflects ultraviolet light (Burkhardt 1982, Wilson and Whelan 1989, Siitari et al. 1999), and Burkhardt (1982) suggested that UV reflection of fruits might affect the foraging behaviour of birds. As green leaves absorb UV light (Fig. 1b), UV reflective fruits should be conspicuous against green foliage (Burkhardt 1982) (Fig. 1c) for frugivores that have cone pigments with sensitivity peaks at both UV and green wavelengths (Altshuler 2001). Originally the wax may have evolved for other functions, for example to protect the fruit from microbes, fungi (Burkhardt 1982) and deleterious radiation of sun. Actually, many fruits appearing black or blue to humans are ultraviolet when taking

into account the UV part of spectrum (the reflectance spectra in Fig. 1). Burkhardt (1982) found that in Germany 14 of 24 species studied (58%) had fruits that reflect UV. In Illinois (USA) the proportion of ultraviolet fruits was 40; 21 of 53 plants species studied having fruits reflecting UV light (Wilson and Whelan 1989). Moreover, a recent study from Panama indicates that 61.5% of species studied (24 of 39) reflected UV light. These tropical fruits lack waxy bloom and their UV reflection is probably due to pigments (Altshuler 2001).

Whether the UV reflection of fruit may affect the detection or preferences of birds is controversial. Wilson and Whelan (1989) in North America and Allen

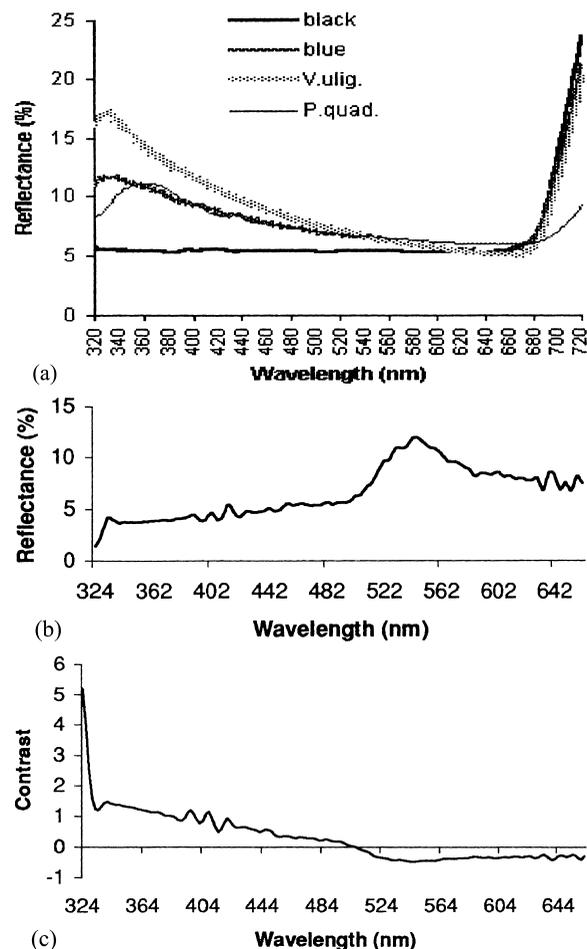


Fig. 1. a) Reflectance spectra of different berries. Explanations: black = a bilberry after the wax layer removed, blue = intact blue bilberry, P.quad. = berry of *Paris quadrifolia* (Liliaceae), V. ulig. = intact blue berry of *Vaccinium uliginosum*. Paris berries do not have waxy coating (own observation). b) Reflectance spectra of a bilberry leaf, *Vaccinium myrtillus*. c) An example of the spectral contrast between bilberries, *Vaccinium myrtillus*, and their background foliage (berry colour (R_s) versus background reflectance (R_b) ratio $[(R_s - R_b)/R_b]$).

and Lee (1992) in New Zealand found no effect of UV reflective waxy bloom on preferences of birds. In a recent field study conducted in Panama, fruit removal was lower when UV was filtered out from ambient light compared to fruit removal from plants under UV transmitting filters or without filters (Altshuler 2001). Moreover, when preferences of redwings (*Turdus iliacus*) on bilberries (*Vaccinium myrtillus*) were studied, a difference was found between the behaviour of adult and naïve birds (Siitari et al. 1999). Both experienced adult and naïve hand-raised juvenile redwings were allowed to choose between blue UV reflecting and manipulated black (wax removed by rubbing) bilberries either in the presence (UV + trial) or absence (UV – trial) of UV light. Adult birds preferred UV reflecting berries in UV + trial, but made no difference between different colour types of berries in UV – trial. However, naïve redwings did not make any difference between the two colour types of berries in either light condition. The experiment showed that UV light may affect foraging decisions of adult redwings and that naïve birds may learn colour preferences e.g. by social learning. It is also possible that the sensory capacity of juveniles is different from that of adult birds. However, the first choice of even naïve birds in this cafeteria test was the UV reflecting berry (Siitari et al. 1999) suggesting that naïve birds could detect UV, too. Also, the black grouse (*Tetrao tetrix*) preferred UV reflecting berries in behavioural experiment (Siitari et al. 2002b), although the location of λ_{max} of the extreme short wavelength-sensitive cone visual pigment in galliform species differs from that in passerines (typically $\sim 360\text{--}370$ nm in passeriformes vs ~ 420 nm in galliformes, Cuthill et al. 2000a). However, the ocular media of birds have a relatively high transmission of short wavelengths and thus permit this cone visual pigment to confer considerable UV sensitivity (Cuthill et al. 2000a), at least in the galliform species studied so far (see references in Cuthill et al. 2000a).

These experiments show that the effect of colour might be strongly context-dependent. In general, environmental conditions during signal transmission and detection affect signal perception (Endler 1993). The bilberry (reflectance spectrum in Fig. 1) is a typical, ubiquitous UV reflecting berry in northern boreal areas of Europe. It grows typically in forest light environment called ‘woodland shade’ in Endler’s classification (Endler 1993). Actually, signal colours in ‘woodland shade’-type of forests should be blue or blue-green and perhaps ultraviolet to maximise brightness (Endler 1993).

As earlier studies have documented that lizards use UV in signalling (Alberts 1989, Fleishman et al. 1993, LeBas and Marshall 2000), challenge for the future research remains to study the possible role of UV in the fruit preferences of frugivorous lizards.

Insect prey and their predators

It has been suggested that birds may also use UV when searching for insect prey (Burkhardt 1982, Jane and Bowmaker 1988). In Finland, most of the night active Lepidoptera (78.6%), but only less than third of the day active species (30.8%), were found to have wing patterns that reflect UV (Lyytinen 2001). Also, in this study, moth wings were manipulated to either reflect or absorb UV, and the survival of these differently treated moths was monitored in the field. Lyytinen (2001) concluded, that UV reflective wing patterns of diurnal Lepidoptera may result in differential survival due to increased predation risk by visually orienting diurnal predators.

Furthermore, when Church et al. (1998a) manipulated the light environment using either UV-blocking or UV-transmitting filters in the laboratory, they found that blue tits (*Parus caeruleus*) tended to detect the cryptic caterpillar prey more quickly in the presence of UV light. As the difference was found only in time needed for first detection, the possibility remains that this behaviour was caused by hesitation due to unnatural illumination. In any case, UV cues of light environment may affect the foraging behaviour of blue tits even when neither prey nor background does reflect large amount of UV. However, if the spectral reflectance of insect prey and its background differs in UV waveband, prey may be highly detectable to birds due to increased contrast between prey and its background.

In cryptic insects the camouflage usually continues also in UV wavelengths, but there are at least some caterpillars that are cryptic in visible light but reflect strongly UV. This may indicate aposematic coloration, advertising unpalatability and/or poisonous qualities (Church et al. 1998b). Therefore, it is also possible that insect larvae may be cryptic to some predators and simultaneously aposematic to others. However, Lyytinen et al. (2001) found that UV cues alone do neither signal unpalatability nor work effectively as aposematic signals to great tits (*Parus major*).

Avian predators and small rodents

In many mammalian species scents form the basis for communication. Scent markings (e.g. urine, faeces and secretions from various glands) play an important role in the social and sexual behaviour of mammals (Johnson 1973, Brown 1979). Scent marks of small rodents are known to be visible in UV light due to fluorescence (Desjardins et al. 1973), as the scent markings absorb part of UV radiation and emit the absorbed energy as visible light. A new finding was that vole scent marks are also detectable in UV light due to reflectance (Viitala et al. 1995, Koivula and Viitala 1999, Fig. 2). Thus predators with ability to detect UV light could use scent marks to find vole patches and assess prey densities.

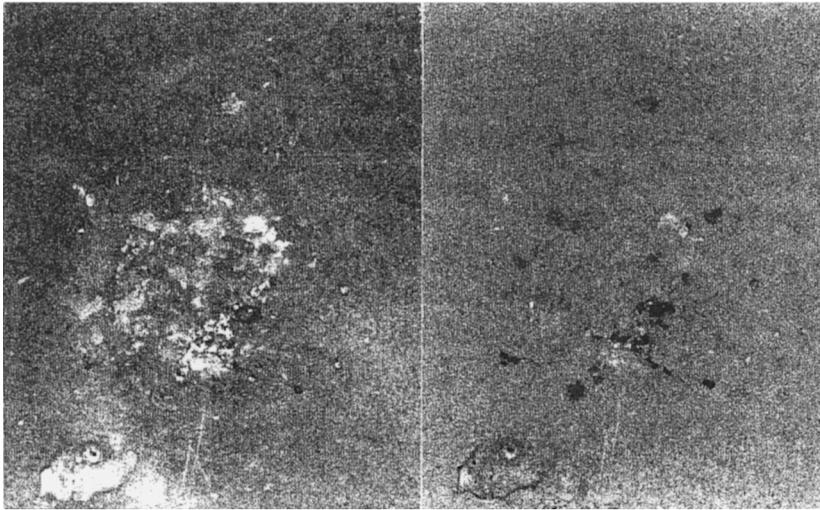


Fig. 2. Scent marks of the field vole, *Microtus agrestis*, in ultraviolet light (left) and in visible light (right).

Both aviary and large scale field experiments have indicated that Eurasian kestrels (*Falco tinnunculus*) are attracted to vole scent marks in the presence of UV light and use them as a cue when hunting (Viitala et al. 1995, Koivula et al. 1999a). In the laboratory experiment kestrels were given a choice among four arenas: 1) vole scent marks in UV light (scent + UV +), 2) clean arena in UV light (scent - UV +), 3) scent marks in visible light (scent + UV -), and 4) clean arena in visible light (scent - UV -). The kestrels were most interested in vole scent marks in UV + condition, measured both as the number of scans (events when the bird pointed its eyes to the target and bobbed its head to estimate the distance) and the time spent above the arenas (Viitala et al. 1995).

UV reflectance of scent marks differs between species and also between reproductive categories of voles, and kestrels may be able to distinguish these differences (Koivula et al. 1999a, b). In a laboratory experiment kestrels preferred the scent marks of mature field vole (*Microtus agrestis*) males over the scent marks of females and non-breeding juveniles. Moreover, kestrels also preferred the scent marks of sibling voles (*Microtus rossiaemeridionalis*) over those of bank voles (*Clethrionomys glareolus*) and field voles. These findings may partly explain why diurnal raptors catch more male than female voles, and why males seem to be more vulnerable prey to rodent-eating birds of prey (Korpimäki 1985, Halle 1988, Mappes et al. 1993). Several studies have also suggested that sibling voles make up a larger proportion of the diet of avian predators than would be expected from the numbers available (Korpimäki 1985, Norrdahl and Korpimäki 1993).

These results are likely to apply to other diurnal birds of prey, too, as field experiments have indicated that rough-legged buzzards (*Buteo lagopus*) are also attracted to vole scent marks (Viitala et al. 1995, Koivula and Viitala 1999). Olfaction or human visible

wavelengths could also have explained the results in the field experiments, but in a controlled aviary environment Viitala et al. (1995) found that kestrels did not react to the scent marks of voles in visible light without UV, and olfactory cues were not important. In the recent laboratory experiment also the great grey shrike (*Lanius excubitor*), a passerine bird feeding mainly on small rodents and insects (Huhtala et al. 1977, Lefranc and Worfolk 1997), showed preference to vole scent marks in presence of UV light (Probst et al. 2002). Perhaps not surprisingly the nocturnal Tengmalm's owls (*Aegolius funereus*) did not respond to vole scent marks either in UV or visible light (Koivula et al. 1997), as the owls may lack UV cones (Bowmaker and Martin 1978), and nocturnal birds of prey probably rely mainly on acoustic cues when hunting.

Densities of small mammals oscillate widely in northern Europe (Hansson and Henttonen 1985). This also affects strongly the breeding densities of birds of prey which vary widely among years and track vole densities without an obvious time lag (Korpimäki and Norrdahl 1991, Korpimäki 1994). During years with low vole densities, kestrels shift to alternative prey, among which shrews, small birds, lizards and insects are most important (Korpimäki and Norrdahl 1991). The ability to visually detect scent marks in UV light may enable diurnal birds of prey to 'screen' large areas in short time and thus find suitable breeding and hunting areas (Viitala et al. 1995, Koivula and Viitala 1999, Koivula et al. 1999b). Altogether, the ability to detect vole scent marks may thus reduce the hunting costs to birds of prey. However, visibility of scent marks in UV light seems not to be too costly for voles. As birds of prey are not as effective predators of voles as small mustelids which use odour cues when hunting (Norrdahl and Korpimäki 1995), the overall predation risk due to visibility in UV light of scent marks is smaller than the risk due to odour of scent marks (Koivula and Korpimäki 2001).

Concluding remarks

The function of ultraviolet vision in foraging of animals is just beginning to be understood. UV cues may enhance food detection where food items either reflect, absorb or scatter UV light in relation to their background (Tovee 1995). All 35 species of diurnal birds, four species of rodents, 11 species of lizards and two species of amphibians studied so far are able to detect UV light. The good ability to detect both visible and UV waveband is likely to allow diurnal raptors to discern scents marks of small rodents and other terrestrial vertebrates. In addition, frugivorous, nectarivorous and insectivorous birds are likely to use UV cues when searching for food. Challenge for future research is a possible role of UV cues in the food preferences of frugivorous and insectivorous lizards as well as insectivorous amphibians. In addition, although there are indications that at least some rodents are sensitive to UV, this subject and its ecological consequences remain to be studied.

An object white to humans is not necessarily white to e.g. birds (Cuthill et al. 2000b). All cone classes of receiver's eye have to be stimulated in relatively similar proportions for an object to be perceived as white in colour. Thus, for a species sensitive to UV, an object should reflect also in UV in order to be perceived as white. As snow reflects UV light, it is not known whether white winter coats of some northern mammals (e.g. arctic hare, *Lepus timidus*) and white plumages of some birds (willow ptarmigan, *Lagopus lagopus*) are more easily detected in UV than in visible light. If some of the camouflage is lost in UV, then the traditional view on a reduction of predation risk due to whiteness should be revised. Moreover, bright coloration and UV visible plumage ornaments may increase predation risk of passerine birds if bird-feeding diurnal raptors (e.g. the sparrow hawks *Accipiter nisus* and the merlins *Falco columbarius*) use these ornaments as a hunting cue.

The possible role of UV cues should be taken into account when food selection of animals is studied, and especially, when artificial food items are provided for study objects. Furthermore, one should be aware of existing light conditions, as spectral range of available light may affect colour perception. In addition, the relative importance of ultraviolet light compared to other wavebands visible to the study object may vary depending on species and visual task in question (Hunt et al. 2001, Kevan et al. 2001, Maddocks et al. 2001).

We suggest that along with laboratory research, field experiments should be conducted to show whether UV sensitivity indeed has importance when wild animals are foraging in natural conditions. Changing the light environment by completely filtering out one waveband from light spectrum, and thus excluding one colour, might result to the target objects appearing unnatural. Thus, we propose future experiments, wherein the colour of

the target objects themselves would be changed and simultaneously the illumination kept or changed in the limits of that in the natural environment of the species studied.

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