

Johanna Honkavaara

ULTRAVIOLET CUES IN FRUIT-FRUGIVORE INTERACTIONS

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ABSTRACT

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Yhteenvedo: Ultraviolettinäön ekologinen merkitys hedelmiä syövien eläinten ja hedelmäkasvien välisissä vuorovaikutussuhteissa

Diss.

All diurnal birds studied so far, many reptiles, amphibians, fish and some rodents are able to detect near-ultraviolet light (UV; 320-400 nm) invisible to humans. In many animals, UV cues have been found to play a role in foraging and mate choice. As many fruits reflect UV light, frugivores sensitive to UV may also use these cues in foraging. Fruit colours and their contrast with background coloration may attract frugivores. In this thesis, I studied the fruit colour preferences of both redwings (*Turdus iliacus*) and small rodents (house mice, *Mus musculus* and bank vole, *Clethrionomys glareolus*). Adult redwings preferred UV reflective berries to black and red ones that do not reflect UV light, regardless of the contrast with the background coloration. Also, ambient light affected their choice, as they preferred UV reflective berries only if UV light was available. However, juvenile redwings did not show any preference between different fruit colours with the exception of preference for UV-blue berries on UV-blue background. However, the colour white was less preferred than the three other colours presented to the juveniles (UV-blue, black and red), possibly as white may signal "edibility" less efficiently than the other colours. Furthermore, redwings changed their initial preferences for artificial UV signals (UV reflective or UV absorbing), after the birds had been taught to associate profitable food with the initially less preferred signal. The results indicate that fruit colour preferences in birds are mainly learned and that innate preference for or avoidance of a colour can be changed by experience. UV reflection of berries may benefit a fruiting plant, like bilberry (*Vaccinium myrtillus*), as my study found that seed ingestion by thrushes, redwings and fieldfares (*Turdus pilaris*), accelerated germination rate and resulted in final germination higher than or similar to that of intact bilberry seeds, although there was within-seasonal and between-year variation in this interaction. When I studied the fruit colour preferences of rodents, I found that UV sensitive house mice used UV cues in foraging when UV light was available, whereas bank voles did not respond to differences in the fruit colours irrespective of the illumination. This might indicate, that bank voles do not detect UV. In sum, this thesis provides further evidence that UV cues are used in fruit-frugivore interactions.

Key words: *Clethrionomys glareolus*; foraging; frugivory; fruit; *Mus musculus*; *Turdus iliacus*; *Turdus pilaris*; ultraviolet; *Vaccinium myrtillus*

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which will be referred to in the text by their Roman numerals. I have written a large proportion of the paper I. I have personally written the papers II, IV-VI and performed most of the work. I have performed a significant proportion of the work for paper III.

- I Honkavaara, J., Koivula, M., Korpimäki, E., Siitari, H. & Viitala, J. 2002: UV vision and foraging in terrestrial vertebrates. *Oikos*, in press.
- II Honkavaara, J., Viitala, J. & Korpimäki, E. 2002: UV sensitivity and foraging in rodents: an experiment with bank voles and house mice. Submitted.
- III Siitari, H., Honkavaara, J. & Viitala, J. 1999: Ultraviolet reflection of berries attracts foraging birds. A laboratory study with redwings (*Turdus iliacus*) and bilberries (*Vaccinium myrtillus*). *Proc. R. Soc. Lond. B* 266: 2125-2130.
- IV Honkavaara, J., Siitari, H. & Viitala, J. 2002: Fruit colour preferences of redwings (*Turdus iliacus*): experiments with hand-raised juveniles and wild-caught adults. Submitted.
- V Honkavaara, J. & Viitala, J. 2002: Initial preference for UV cues in redwings can be altered by experience. Manuscript.
- VI Honkavaara, J., Siitari, H., Saloranta, V. & Viitala, J. 2002: Avian seed ingestion changes germination patterns of bilberry, *Vaccinium myrtillus*. Manuscript.

1 INTRODUCTION

1.1 Colour vision in terrestrial vertebrates

Vision is utilised in many behaviours like foraging, mate choice and predator avoidance. In nature, there are a huge variety of photic environments, and animal species have to adjust to the specific light conditions in their habitat, for example, the darkness of deep sea or the brightness of the desert. To optimise the use of available light, diverse visual systems have evolved as adaptations to specific ecological settings. Thus, the size and shape of eyes, photoreceptor organisation and colour sensitivity provided by visual pigments can differ depending on the photic environment inhabited by a species. For example, variation in the visual pigments of fish relate to the various photic environments found in different water habitats (Yokoyama & Yokoyama 1996 and references therein).

The vision in most vertebrates is based on a set of photosensitive molecules, i.e. visual pigments, in two types of photoreceptor cells called rods and cones. Rod cells are more sensitive to light than cones and are used in low-light conditions, whereas cones are used in bright-light conditions and contribute to colour vision. In order to perceive colour, an animal has to possess at least two types of cones with different spectral sensitivities, as colour perception is a result of the summation of neural outputs from different cone types. In addition to cone types, colour perception is determined by the neural processing of the received visual information (Bradbury & Vehrencamp 1998).

The original type of colour vision in terrestrial vertebrates is probably based on four cone photopigments, i.e. potential for perception of four primary colours and their combinations (Robinson 1994). All diurnal birds studied, many reptiles and amphibians seem to possess tetrachromatic colour vision (Fleishman et al. 1993, Loew 1994, Harosi 1994, Deutschlander & Phillips 1995, Ellingson et al. 1995, Loew et al. 1996, Cuthill et al. 2000). In addition to cones sensitive to blue, green and red light, these animals have a cone type sensitive to near-ultraviolet light (UV, 320-400 nm) invisible to humans. Moreover, the

tetrachromatic eye of some terrestrial vertebrates, including birds, possesses oil droplets connected to the cone cells. These differently coloured oil droplets filter the light of certain wavelengths, and thereby are suggested to increase colour saturation, enhance colour discrimination and improve colour constancy (Bowmaker 1980, Jane & Bowmaker 1988, references in Cuthill et al. 2000).

Humans, Old World primates and some New World primates have trichromatic colour vision. However, most mammals are dichromatic. They have two cone photopigment types, one with a peak absorbance at 420-450 nm and the other with a peak at 500 nm or longer. For some rodents, the cone type sensitive to shorter wavelengths has a maximum absorbance at about 360 nm, and thus they are sensitive to UV light. These species are house mouse (*Mus musculus*), brown rat (*Rattus norvegicus*), Mongolian gerbil (*Meriones unguiculatus*) and Botta's pocket gopher (*Thomomys bottae*). They are unique among mammals, as no other mammalian species are known to be able to detect UV. Some mammals have only one type of cone photopigment, and thus lack colour vision (Jacobs 1993 and references therein).

1.2 UV sensitivity in foraging (I)

The ability to detect UV light may play a role in navigation and orientation, in social signalling and in foraging (e.g. Bennett & Cuthill 1994). The significance of UV cues in mate choice has been established especially for birds and also for some lizard and fish species (e.g. Bennett et al. 1996, 1997, Andersson et al. 1998, LeBas & Marshall 2000, Siitari et al. 2002a, Kodric-Brown & Johnson 2002). In avian foraging, the importance of UV vision has also received some attention (e.g. Burkhardt 1982, Willson & Whelan 1989, Viitala et al. 1995, Church et al. 1998a, Siitari et al. 2002b). As food items may either reflect, absorb or scatter UV in relation to their background, the UV cues of both food items and/or their environment may be used in food detection (Tovée 1995). At dusk and dawn, when many rodents are active, a high proportion of available light is of short wavelengths (Lythgoe 1979, Endler 1993). Thus, animals active at these times of day might use UV wavelengths in different visual tasks, e.g. in foraging (Bennett & Cuthill 1994). Although some rodent species are found to be able to detect UV light, the ecological context of this ability has not yet been studied.

1.1.1 UV sensitivity in predator-prey interactions

UV cues increase predation risk due to avian predators. UV reflectance of wing patterns in day-active Lepidoptera moths may result in differential survival compared to the moths with UV absorbing wing patterns (Lyytinen 2001). Moreover, when UV light was available, blue tits (*Parus caeruleus*) found cryptic caterpillar prey more quickly (Church et al. 1998a). Most cryptic insects extend their camouflage to the UV wavelength area, but some species are cryptic only in visible light (i.e. to most mammals) while reflecting UV. This might function

as an aposematic coloration for avian predators indicating unpalatability or toxicity (Church et al. 1998b), although UV cues alone do not signal unpalatability nor do they work effectively as aposematic signals, at least not for great tits (*Parus major*) (Lyytinen et al. 2001).

For mammalian prey species, some evidence has been presented that the UV reflecting scent marks (e.g. urine, faeces and secretion from various glands) of small rodents attract diurnal raptors, like kestrels, buzzards and even a passerine the great grey shrike (*Lanius excubitor*) (Viitala et al. 1995, Koivula & Viitala 1999, Probst et al. 2002). Using UV cues, diurnal birds of prey are able to scan for potential hunting areas for voles. In contrast to diurnal raptors, nocturnal Tengmalm's owls (*Aegolius funereus*) do not respond to UV reflective scent marks (Koivula et al. 1997). Owls probably lack UV cones (Bowmaker & Martin 1978) and hunt using mainly acoustic cues. Although diurnal raptors seem to be able to distinguish even between species and reproductive categories of voles since their scent marks differ in UV reflectance (Koivula et al. 1999a, 1999b), the predation risk induced by scent marks visible to birds is likely to be smaller than the risk caused by olfactory cues of scent marks attracting small mustelids (Koivula & Korpimäki 2001).

1.1.2 UV sensitivity in fruit-frugivore interactions

Nectarivorous and frugivorous birds may also use UV cues. As many flowers have UV reflecting or absorbing patterns in their petals, hummingbirds may use these patterns as foraging cues (Huth & Burkhardt 1972). Furthermore, as many fruits and berries reflect UV, this property may contribute to frugivory (Burkhardt 1982). When UV reflectance of fruit was measured, 40-58 % of species studied reflected UV in temperate habitats (Burkhardt 1982, Willson & Whelan 1989) and 61% on a tropical island (Altshuler 2001). In the first field studies on the effect of UV reflectance on avian fruit preferences, birds did not seem to use UV cues in fruit selection (Willson & Whelan 1989, Allen & Lee 1992). In a recent field study with the UV reflective fruit of *Psychotria emetica*, rate of fruit removal was lower when ambient UV light was removed from the fruiting display (Altshuler 2001). In a behavioural experiment, black grouse (*Tetrao tetrix*) preferred UV reflective blue bilberries to non-UV reflective black ones when UV light was available in the illumination, but no preference for either colour morph was observed when UV light was absent (Siitari et al. 2002b).

In the research on fruit-frugivore interactions, fruit colours have been suggested to advertise fruit to avian seed dispersers. In addition, contrast of the fruit colour with the background coloration has been associated with attraction of avian frugivores (Willson & Whelan 1990, Whelan & Willson 1994, Burns & Dalen 2002). The effectiveness of a fruit colour as an advertisement may vary due to the reflectance spectrum of the fruit colour, the ambient light spectrum, the transmission properties of air and the veiling light spectrum, and also the sensory capacity of the receiver. In addition, the magnitude of colour and brightness contrasts may vary due to the light conditions (Endler 1990, Endler

1993). Thus, depending on the fruiting environment and the visual abilities of the seed disperser species, the most effective colour of fruit (and any accessory fruiting display) may vary between habitats. Thus, when avian fruit colour preferences are studied, the visual abilities of the birds have to be considered and the light conditions should be controlled. Also, the individual experience with differently coloured fruit in nature may override any innate preferences of naive birds (Willson & Whelan 1990). Possibly due to these facts, previous studies on fruit colour preferences of birds have detected considerable within- and between-species variation (e.g. Willson et al. 1990, Willson 1994).

Certain fruit colours have been associated with specific seed disperser taxa e.g. red, black and blue have been considered to be colours of typical bird-dispersed fruit species while green, yellow or white fruit are more likely to be eaten by mammals (reviewed by Murray 1986). However, many fruits are eaten by various taxa with differential sensory capacities. For example, UV-blue bilberries (*Vaccinium myrtillus*) are consumed not only by birds, but also by small rodents, bears, foxes etc. Furthermore, the effectiveness of various fruit-eating species as seed dispersers may differ, even within a taxon e.g. between bird species. For example, variation in the treatment provided by the digestive apparatus of a species (e.g. teeth, gut), the microhabitat in which the seeds are dispersed and the distance of dispersal from the fruiting plant may result in differences in seed germination success and seedling survival between the seeds dispersed by different animal species (Schupp 1993). In addition, some frugivores are seed predators rather than seed dispersers. Thus, to evaluate a frugivore as a seed disperser for a certain plant species, more information is needed on the interaction than just the observation of the frugivore eating the fruit of the given species.

1.3 The aim of the thesis

The aim of this thesis was to obtain further information on the significance of UV cues in foraging. In particular, I have studied the importance of colour cues in frugivory.

In the first paper, I have reviewed the recent knowledge of UV sensitivity and its importance in foraging by terrestrial vertebrates. In the second and third paper, I have studied whether the absence or presence of UV light affects the fruit colour preferences of small rodents (II) and thrushes (III). In the fourth paper I investigated whether hand-raised juvenile redwings prefer certain fruit colours *per se* and if the interaction with fruit colour and contrasting background coloration affect the fruit colour preferences of both experienced adult and naive juvenile redwings. In the fifth paper, I examined whether redwings prefer UV cues *per se*, and if their initial preferences could be changed. Finally, in the sixth paper, I studied the effects of avian gut passage on the germination success of bilberry seeds and further, if there is any within-season and between-year variation in this interaction.

2 MATERIALS AND METHODS

2.1 Study species

In the second paper (II), I used house mice (*Mus musculus*) and bank voles (*Clethrionomys glareolus*) as study objects. Both rodent species include berries in their natural diet. House mice are known to have a cone photopigment type sensitive to UV light. They have also been shown to be able to use UV in forced-choice discrimination task with light panels (Jacobs et al. 1991). On the other hand, the physiological capacity of bank voles to detect UV light has not been previously studied. The house mice were provided by the Finnish Forest Research Institute, Vantaa Research Centre, Ojajoki Field Station. I trapped the bank voles with Ugglan multiple-capture live-traps near the Konnevesi Research Station in Central Finland.

The study species in the experiments on UV sensitivity and avian foraging was the redwing (*Turdus iliacus*) (papers III, IV, V, and also the germination experiment VI). In Finland, this turdid species is abundant in summer, as they migrate here to breed. Redwings are omnivorous and include both insects and berries in their diet. Another turdid used was the fieldfare (*Turdus pilaris*) (in the germination experiment, VI), which also consumes considerable amounts of berries. Unfortunately, there is no physiological data available on the cone photopigment types of redwings. However, for blackbirds (*Turdus merula*) evidence on UV sensitivity exists (Hart et al. 2000). As all the day-active passerines studied so far have been found to possess a UV sensitive cone type, redwing most probably have such cones also. In experiments with redwings, both wild-caught adult and hand-raised juveniles were used. The adults were mistnetted (within 70 km of Konnevesi Research Station), and their broods were collected and raised in captivity. For the germination experiment (VI), fieldfare chicks were collected from their nests when they were about 10-13 days old and hand-raised in captivity.

Bilberries (*Vaccinium myrtillus*) were used in all the experiments conducted with berries. In boreal forests, it is a very common clonal shrub

species with abundant berry crops. The most common morph of bilberry has a UV reflective wax layer, and appears bluish to the human eye. Another, much less abundant, morph is black. As some other characteristics, in addition to colour (e.g. taste), may vary between the morphs, I used only berries of the bluish morph in the berry choice experiments (II, III, IV). The “black” bilberries were achieved by rubbing the wax off gently, and the “UV-blue/UV-reflecting/intact” ones were unrubbed berries of the bluish morph. In addition to bilberries, red and white currants (*Ribes* spp.), which are widely cultivated in Finland, were also used for the experiments reported in the fourth paper. The bilberries were collected from the Konnevesi area, and the currants were obtained from an orchard in Muurame, Central Finland.

The colours of the berry types, backgrounds and artificial signals used in the experiments were measured with a calibrated spectroradiometer (EG&G Gamma Scientific GS3100 Radiometer with xenon fibre optic light source RS-22UV). The illuminations were measured with the same spectroradiometer, using a miniature cosinus receptor (EG&G 700-8D, 250-1700 nm) without a standard light source.

2.2 Laboratory experiment with house mice and bank voles (II)

In the second paper, I examined whether or not rodents use UV cues in foraging. I performed the experiment with house mice and bank voles in four sheet metal arenas (1.00 x 0.53 x 0.50 m). The experimental room (13.3 m²) was illuminated with four fluorescent tubes (two True-lite II, Duro Test, 58W 5500/96 and two True light 56W/5500). In addition, two bulbs (Black light blue; emitting mainly between 300-400 nm) were placed above two of the four arenas, one bulb above each arena. These arenas were also covered with UV-transmitting filters (transmitting most of the wavelengths between 320-700 nm. The transmission curve is presented in paper II). The two arenas not under the bulbs were covered with UV blocking filters (transmitting most of the wavelengths between 400-700 nm but blocking most of UV wavelengths. The transmission curve is presented in paper II). Thus, I achieved two different light environments, one with UV light present (UV+) and the other with UV light absent (UV-).

In the arenas, I placed 32 bilberries still attached to the vegetative shoots. The shoots were placed in holes drilled in a wooden plate (0.25 x 0.125 x 0.02 cm), eight UV-blue and eight black berries to different short sides of each plate, altogether 16 berries on each plate. The colour types were thus separated by 9 cm. I placed one plate in both short sides of each arena. For the first trial of each rodent, I randomised the position of the plate (one colour morph on the left and one on the right) in each side. In the second trial for each rodent, I used the mirror image of this position.

The bank voles could have had previous experience with bilberries in nature, whereas the house mice were bred in captivity and had no previous

contact with natural berries. Therefore, before the experiment, I offered berries of both colour types to both rodent species as part of their diet. During the experiment, I released each rodent twice in the arenas; once in an arena with UV light present and once in an arena without UV light, in randomised order. The duration of a trial was one hour for bank voles. For house mice, a trial lasted on average 3 to 6 hours, depending on the foraging activity of each animal. After the trial, I removed the animal from the arena, and counted the amount of damaged or eaten (i.e. chosen) berries of each colour type. I compared the proportions of the chosen UV-blue berries and the proportions of the chosen black berries in the two different light conditions, respectively. The two rodent species were analysed separately.

2.3 Laboratory experiments with redwings (III, IV, V)

In three papers of this thesis (III, IV, V), the colour preferences of redwings were tested. In these experiments both wild-caught (having previous experience with berries in nature) adults and hand-raised (naive with berries) juvenile birds were used. All the experiments were conducted in indoor cages (0.64x 0.69x 0.71m), which were painted matt black with very low reflectance in all wavelengths of light. In each of these three papers, I ranked the choosing order of the signal or berry colour and used the scores in statistical tests. Since the choosing order might reflect the preferences of the birds, the first choices were given the highest scores and the last choices the lowest scores.

In the third paper, we studied if the berry colour choices of redwings vary due to different levels of ultraviolet light in the illumination. The experimental cages were illuminated with a solarium tube (Osram Eversun L 40W/79K) and a day-light tube (Osram Biolux L 18W/72). The level of UV light in the cages was manipulated using UV transmitting (UV light present in the illumination) and UV blocking (UV absent) filters. The birds were offered four UV reflecting and four black berries on a tray covered with the green leaves of grey alder (*Alnus incana*), once in each illumination (UV present and UV absent). We used both wild-caught adults and hand-raised juveniles in this experiment to examine if learning (i.e. previous experience with berries) affects preferences.

In the fourth paper, I examined first if juveniles prefer any berry colour to others when encountering simultaneously black, UV-blue, red and white berries, one of each colour, on green leaves (of grey alder). Secondly, I offered a new set of juveniles one red and one white berry on green leaves in five consecutive trials. Thirdly, I studied if contrast between berry colour and its background coloration affects colour preferences and if previous experience plays a role in this visual task. Thus, this third experiment was conducted with both wild-caught adults and hand-raised juveniles. Here, I offered the birds five UV-blue and five red berries once on each of three background colorations: UV-blue (made from a blue computer mouse pad covered with UV-reflecting white chalk), red (covered with red plastic) and green (covered with green leaves of

grey alder). In these three experiments, the experimental cages were illuminated with day-light tubes (Osram Biolux L18W/72-965).

In the fifth paper, my aim was to study if redwings prefer UV cues *per se* and if they can learn to change their preferences using UV cues. I used artificial signals associated with live food, in this case, mealworms. I prepared two types of signals using white silk paper. For a UV reflecting signal (UV+ signal), silk paper was covered with white chalk, which reflects UV light. A second signal was prepared by covering the silk paper with TiO₂, which absorbs UV light (UV- signal) (method adopted from Lyytinen et al. 2001). Both signal types appeared white to the human eye. The signals were placed on the lids of plastic cups. I clipped a hole to each lid, so that the birds were able to eat from the cups. The cups were sunken into a plastic tray. On each tray, I placed two cups, one of each signal type. In the trial, each bird encountered three consecutive trays with a mealworm in each cup. After testing for initial preference, the birds were divided to two groups on the basis of their preference. Then, I placed five mealworms in the cup associated with the less preferred signal and left the cup with the more preferred signal empty. Each bird encountered three consecutive trays, on three separate occasions. Then I tested the final preferences in same format as undertaken to test for the initial preference. The experimental cages were illuminated with day-light tubes for these tests (Osram Biolux L18W/72-965).

2.4 Germination experiment with bilberries (VI)

In the paper VI, I studied the effects of avian seed ingestion and the subsequent gut passage on the germination patterns of bilberry seeds. I also investigated whether the timing of seed collection within the fruiting season affects the germination patterns and whether there is between-year variation in these effects. Redwings (in 1999) and fieldfares (in 1997) were the frugivores used in this experiment. The birds were offered bilberries, and the passed seeds were collected from the faeces. Seeds were also collected from intact (not ingested) berries. I collected the berries used in the experiment from the Konnevesi area between late July and late September (depending on the year); three times during the fruiting season in 1997 and 1999. The seeds were germinated on Petri dishes in indoor growing chambers. I monitored the seeds for radicle emergence on 14th, 20th and 26th day after the start of the germination experiment. The data collected in 1997 and 1999 were analysed separately. I tested for the effects of treatment (ingested and intact) and proceeding of the fruiting season on the germination success on each control date (14th, 20th and 26th day), separately. I also tested for any difference in the germination success between treatments on each control date and for each time in the season, separately.

3 RESULTS AND DISCUSSION

3.1 UV-vision and foraging in house mice and bank voles (II)

When UV light was available, house mice ate more black berries than UV-blue berries. However, they ate similar amounts of both colour types, when UV light was absent from the illumination. In contrast, differences in the illumination did not affect bank vole behaviour and they showed no colour preference. This result provides more behavioural evidence that house mice can detect UV light and that they are able to use UV cues in foraging. In contrast, bank voles probably do not use UV cues when discriminating between food items. However, on the basis of this experiment, I cannot exclude the possibility that bank voles are also sensitive to UV light. To confirm this, physiological studies on their cone photopigment types would be necessary.

The preferences of house mice in this experiment might be due to either avoidance of UV reflective food items or preference for UV absorbing ones. Many natural food items of house mice, like fleshy roots, stems, green leaves and most seeds absorb UV light. However, some seeds and insects, that are unpalatable or even toxic, may reflect UV light. Thus, house mice may show neophobic reaction to new UV reflective food items unfamiliar to them. Or in contrast, they prefer UV absorbing food items like black bilberries. Nevertheless, although crepuscular and nocturnal rodents probably use olfactory cues as their principal guide when searching for food, the results show that the UV sensitivity of rodents may play some role in foraging.

It is not clear, whether or not UV sensitivity contributes to colour vision in house mice. Typically for nocturnal organisms, house mice have more rod than cone cells in the eye's retina to maximise sensitivity to available light (Yokoyama & Yokoyama 1996). House mice have two types of cone photopigments: a middle wavelength sensitive (MWS) and an extremely short wavelength sensitive (UWS, maximally sensitive to UV) (Jacobs et al. 1991). Uniquely among vertebrates, there is a large scale topographic separation in the distribution of the cone types in the retina. They are distributed on opposite

halves of the eye (Szél et al. 1992) so that the dorsal retina is mostly populated by MWS cones, whereas the ventral retina is solely occupied by UVS cones in unusually high density. This segregation may decrease the likelihood that possession of two cone types automatically contributes to colour vision in house mice (Jacobs 1993). The function of this separation is unclear, although it may correlate with the fact that middle wavelengths are abundant at the ground level, whereas the light coming from above is rich in short wavelengths (Szél et al. 1992). Possibly, UV cues may contribute to perceived differences in brightness by house mouse. This might also be possible for bank voles, as the sensitivity range of their SWS cones may reach into UV waveband even though they probably do not have cones maximally sensitive to UV (Jacobs GH, personal communication).

It has been suggested that the UV reflectance of fleshy fruit may serve to advertise fruit to seed dispersers (Burkhardt 1982), both UV sensitive birds and rodents (Altshuler 2001). According to our results, UV reflectance does not attract foraging rodents, at least not house mice. In fact, only a few rodent species have been found to be sensitive to UV light (Jacobs 1993) and most rodents are mainly seed eaters. Thus, they probably are rather detrimental than beneficial to fruiting plants unless the plant species rely on scatter-hoarding rodents in seed dispersal, which is unlikely in the case of fleshy fruit. Nevertheless, as some rodents have UV sensitive cones in the eye's retina and are able to use UV cues in various tasks (Jacobs et al. 1991, Jacobs & Deegan II 1994, this experiment (II)), the ecological context and significance of UV sensitivity in rodents remains to be determined in more detail.

3.2 UV sensitivity and foraging in redwings (III, IV, V)

Adult redwings preferred UV-reflective bilberries over black ones, when UV light was included in the illumination (III). However, when UV light was blocked out with a filter, the adult birds ate both colour morphs in similar amounts. UV-reflective berries also got higher scores in the trial with UV light present compared to the trial with UV light absent. For juveniles, no preference for a berry colour type was found in either UV present or UV absent conditions.

When juvenile naive redwings were offered four different berry colours simultaneously (IV), they showed no preference between UV-blue, black and red berries. However, they preferred these three colours to white. In addition, their first choice was random in this trial. In the pairwise trial, a new set of naive juveniles strongly preferred red berries to white. They also chose the red berry first. These results indicate that juvenile birds have innate, not learned, bias to reject white. Possibly, white colour does not signal that a berry is edible as effectively as red, black or UV-blue. Also, white colour in fruit may indicate unripeness, as white colour in bird-dispersed ripe fruit is less common than the other three colours. Moreover, berry choices of redwings were not affected by the contrast in hue between the berry colour and its background coloration.

Adult redwings preferred UV-blue berries over red ones on all three background colorations (UV-blue, red and green). However, the naive juveniles preferred UV-blue berries over red ones only on UV-blue background. On the other two backgrounds no preference for either colour was found.

Adult birds have most likely had experience with both berry types in nature, and thus learned to prefer UV-blue bilberries over black bilberries (III) and over red currants (IV). Moreover, the UV-blue bilberry is more common in nature than the black morph, and thus birds were probably more familiar with the UV-blue morph and this may have directed their choice. It does seem that juveniles are attracted to UV-blue berries to some extent, but they probably have to learn to associate each colour with other features of a berry species like taste or nutritional content. This might be achieved by social learning i.e. mimicking adults in flocks and/or individual learning through trial and error. Another explanation for the difference between the two groups is that the sensory capacity of juveniles may differ from that of adults. However, this does not automatically mean they would lack the ability to detect UV light, especially as the juveniles preferred UV-blue berries on a UV-blue background (IV). These results indicate, that UV reflection of fruit may attract birds, at least in light environments rich in short wavelengths. In these kind of habitats signal colours should be blue, blue-green or perhaps ultraviolet to maximise their brightness (Endler 1993). Thus, UV reflective coloration may efficiently advertise fruit to potential seed dispersers sensitive to UV light.

The contrast with the background coloration may draw the attention of seed dispersers to the fruit colour itself. Osorio et al. (1999) suggest that the main function of contrast might be to draw the attention of a receiver to the stimulus, whereas more accurate information is provided by the colour of the object itself. Even if contrasting structures were only noninformative accessory stimuli themselves, multicomponent signals may be more easily detected, discriminated and remembered (Rowe 1999). Therefore, contrasts may function as foraging cues more efficiently when viewed from a distance rather than the close range of encounter used in this experiment. In a field study by Whelan & Willson (1994), both fruit removal rate and proportion of fruit removed were higher from bicoloured than unicoloured fruiting displays. In my experiment (IV), previous experience of adult birds with the berry species presented had probably determined their foraging decisions rather than colour contrast. For juveniles, which are learning to forage, their sampling behaviour may have been more random, and thus no effect of contrast was observed.

When redwings were presented with artificial UV signals (V), as a group they preferred neither the UV reflecting nor the UV absorbing signal. No difference was found between juveniles and adults. However, there were considerable individual differences in the initial preferences. After the attempt to teach the birds to select the initially less preferred signal the birds preferred neither of the signals, although their preferences for the initially less preferred signal had changed. The results indicate, that the preferences are not fixed but can be changed with experience. Redwings seem to lack any obvious preference for UV cues *per se*. In the case of palatable and non-toxic food items, learning to

associate a colour with their other properties, e.g. nutritional content, might be biologically more relevant than innate preference for a colour *per se*. Furthermore, in terms of visually guided behaviours, the relative importance of different wavelengths in available light probably varies depending on the task in question (e.g. Hunt et al. 2001, Kevan et al. 2001, Maddocks et al. 2001) or the context of presentation (Gamberale-Stille 2001).

3.3 Effects of seed ingestion on germination patterns of bilberry (VI)

In seasonal environments, the timing of seed collection seems to affect the results of germination studies. The bilberry seeds collected early in the fruiting season germinated faster than seeds collected later in the season. Seed ingestion by birds accelerated germination, as the passed seeds germinated faster than intact seeds (i.e. seeds collected from the berries by hand). An exception to these results were seeds collected in late July 1999, wherein no differences were found between treatments. The passed seeds had final germination percentage higher than or similar to that of intact seeds. The final germination percentage did not differ between seed collection dates for intact seeds nor for passed seeds.

The cause for the hastened germination rate by bird ingestion might be the changes in dormancy patterns caused by chemical and/or mechanical abrasion of the seed coat during the gut passage. If faster germination results in better seedling survival, ingestion by birds might benefit bilberry in habitat recruitment. However, faster germination does not automatically guarantee better survival of the seedlings in unfavourable conditions. Moreover, post-dispersal seed predation or seedling herbivory might counterbalance any benefits from gut passage (Traveset et al. 2001). In any case, seed dispersal over long distances by animals may outweigh potential defects caused by gut treatment. Although bilberry disperses locally by clonal growth, it relies on seed dispersal by mammals and birds in recruiting new habitats. As ingestion by birds has no obvious detrimental effects on seed germination, the UV reflecting wax layer of bilberries attracting avian seed dispersers (III) may benefit the plant by increasing the consumption of berries by birds.

The results indicate that in experiments performed in seasonal environments, the timing of seed collection should be planned carefully and reported, as the timing may affect the results and thus also the interpretations of the effect of frugivores in germination success. In addition, there may be between-year variation in these effects.

4 CONCLUSIONS

Fruit colours may attract frugivores, especially avian seed dispersers. The contrast of fruit colour with background coloration may also increase fruit conspicuousness to fruit-eaters. According to my results, fruit colour preferences in birds are mainly due to learning to associate preferred colours with other properties of fruit (III, IV, V). Adult birds had strong preferences for UV-reflecting berries over black and red berries, regardless of contrast with the background coloration. In addition to fruit colour, the choices of adults were affected by ambient light, as they did not show any preference between UV-blue and black berries, when UV light was not available (III). In contrast, juvenile birds did not prefer any fruit colour irrespective of the illumination used (III). However, they preferred UV-blue berries over red ones on a UV-blue background. When berries were presented on green or red backgrounds, juveniles did not reveal a preference (IV). However, white berries were less favoured than other berry colours (red, black and UV-blue). This may be caused by some innate rejection of white, possibly as an indication of unripe fruit. Alternatively, the white colour may signal edibility less efficiently compared to the other three colours. In nature, such initial preferences are probably overridden by individual experience with white fruit. Moreover, innate preference or avoidance of a colour may be context-dependent. In an experimental study, naive chicks did not react differently to red and green fruit-like stimuli, but preferred green insects over red ones. In fruits red colour signals profitability, while among insects red is used as a warning colour (Gamberale-Stille & Tullberg 2001).

The results of paper II provide additional behavioural evidence that house mice are able to detect UV light and that they can use UV cues in foraging. Although voles did not respond to differences in UV reflectance of food items (when presented with UV-blue and black berries), on the basis of this experiment I can not conclude that they lack UV sensitivity. To establish this assumption, research on the cone photopigment types of voles is needed. Although rodents probably rely mainly on olfactory cues in search of food, the ability to detect UV light might have some ecological significance in foraging or in other visually mediated tasks.

In light of recent knowledge, mutual selection pressures between plants and their seed dispersers are greatly constrained (Levey & Benkman 1999). Along with the hypotheses pertaining to the attraction of dispersal agents, other adaptive hypotheses presented for the evolution of fruit colour include defence and physiological requirements, physiological and phylogenetical constraints, and selection on other correlated characters (Willson & Whelan 1990). In addition to fruit colour, a suite of characteristics in fruit may affect the foraging choices of frugivores e.g. nutritional constituents (reviewed by Levey & Martinez del Rio 2001), secondary metabolites (Cipollini & Levey 1997) and fruit pulpiness (i.e. pulp-to-seed ratio) (Sallabanks 1993).

Although the ultimate function of fruit colours may not be the attraction of frugivores, if a certain colour is more easily detected in the habitat of the fruiting species and frugivores learn to associate the colour with other favourable properties of the fruit, then the colour may contribute to higher removal rate of the fruit and thus enhanced seed dispersal. Furthermore, birds provide long-distance dispersal of seeds and the means to disperse sexually produced offspring in addition to reproduction by clonal growth. In the case of bilberry, seed ingestion by birds hastened the germination of seeds. The final germination percentage of seeds passed through the intestinal tracts of thrushes was higher than or similar to that of intact seeds (VI). However, there was within-season and between-year variation in these interactions. The UV reflection of the wax layer in berries may benefit bilberry by attracting birds to ingest berries and thereby disperse the seeds.

The research on the importance of colour vision in visually guided behaviours has addressed the need for objective measurement of colour and consideration of the species-specific visual abilities of study objects along with the differences in neural processing of the visual information (e.g. Cuthill et al. 2000, Kevan et al. 2001) and in receiver psychology (e.g. Jones et al. 2001). Moreover, the importance of different wavelengths may vary with behaviour (e.g. Maddocks et al. 2001). Thereby, when conducting behavioural experiments in the laboratory with artificial illumination, any deviation from the illumination in natural environment should be taken into account. Although knowledge on the significance of UV cues in foraging has accumulated during the last decade, many interesting questions remain unstudied.

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YHTEENVETO

Ultraviolettinäön ekologinen merkitys hedelmiä syövien eläinten ja hedelmäkasvien välisissä vuorovaikutussuhteissa

Eläimet hyödyntävät näköaistiaan monissa eri tehtävissä, kuten etsiessään ravintoa tai sopivaa parittelukumppania. Monet maaselkärangaiset, kuten useat päiväaktiiviset lintulajit, monet liskot ja sammakkoeläimet sekä neljä jyr sijälajia pystyvät aistimaan lähiultraviolettia valoa (UV-A; elektromagneettista säteilyä aallonpituusalueella 320-400 nm), jota ihmissilmä ei havaitse. Lisäksi useimmat näistä eläimistä havaitsevat myös sinistä, punaista ja vihreää valoa eli ihmiselle näkyvää valoa (aallonpituusvälillä 400-700 nm). Kuitenkin suurin osa nisäkkäistä, mukaan lukien pääosa jyr sijöistä, kykenee aistimaan vain sinistä sekä vihreää valoa. Erityisesti lintujen kykyä aistia ultraviolettivaloa on tutkittu ahkerasti viime vuosina. Tutkimusten mukaan linnut hyödyntävät UV-näköään ainakin ravinnonvalinnassa ja puolisonvalinnassa, mahdollisesti myös suunnistamisessa. Myös liskojen ja kalojen on todettu hyödyntävän UV-valoa heijastavia ornamentteja puolisonvalinnassa. Jyr sijöiden UV-näön ekologista merkitystä ei kuitenkaan ole vielä tutkittu.

Yleisesti on esitetty, että hedelmien värit houkuttelevat tehokkaasti hedelmiä syöviä eläimiä, jotka toimivat siementen levittäjinä. Hedelmänvärin kontrasti taustaympäristön värin kanssa saattaa lisätä värin houkuttavuutta. Lisäksi hedelmäkasvin kasvuympäristön valaistusolot sekä hedelmänsyöjäeläinten värienerotuskyky voivat vaikuttaa siihen, mitkä hedelmien värit ovat eri ympäristöissä helpoimmin havaittavissa. Monet hedelmät ja marjat heijastavat ultraviolettia valoa, ja tämä ominaisuus saattaa houkuttaa UV-valolle herkkiä siementenlevittäjiä etenkin sellaisissa kasvuympäristöissä, joissa ultraviolettivaloa on suhteellisen paljon käytettävissä. Väitöskirjatyössäni tutkin, miten marjojen eri värit, niiden kontrastit taustavärien kanssa sekä valaistusolot vaikuttavat marjoja syövien eläinten ravinnonvalintaan. Tutkimuksissani käytin mustikoita (*Vaccinium myrtillus*) ja viinimarjoja (*Ribes* spp.). Mustikan sinisen marjan vahapeite heijastaa myös ultraviolettia valoa, kun taas vahapeitteetön ns. tervamustikka on väriltään musta. Vahapeite voidaan myös pyyhkiä pois, jolloin tuloksena on tervamustikkaa vastaava musta marja. Käytin kokeissani pyyhittyjä marjoja, etteivät mahdolliset makuerot eri mustikkatyyppien välillä vaikuta tuloksiin. Lisäksi käytin valintakokeissani punaisia ja valkoisia viinimarjoja.

Väitöskirjani ensimmäiseen osatyöhön olen kerännyt tämänhetkistä tutkimustietoa ultraviolettivalon hyödyntämisestä maaselkärangasten ravinnonvalinnassa. Toisessa osatyössä tutkin kokeellisesti, käyttävätkö jyr sijät ultraviolettia valoa ravinnonvalinnassa. Tässä kokeessa käytin sekä kotihiiriä, joiden tiedetään aistivan UV-valoa, että metsämyyriä, joiden UV-näöstä ei ole tutkittua tietoa. Kotihiiret söivät enemmän mustia kuin UV-valoa heijastavia sinisiä marjoja, kun UV-valoa oli valaistuksessa mukana. Kun UV-valo poistettiin, hiiret söivät molempia marjatyyppejä yhtä paljon. Metsämyyrä söi molempia marjatyyppejä yhtä paljon valaistuksesta riippumatta. Tämä viittaisi siihen, et-

tei metsämyyrä näe UV-valoa, tosin tämä täytyisi varmistaa silmän fysiologisilla tutkimuksilla. Kotihiiri sitä vastoin pystyi hyödyntämään UV-valoa ravintoa etsiessään.

Seuraavissa osatöissä tutkin, käyttävätkö punakylkirastaat (*Turdus iliacus*) ultraviolettivaloa marjanvalinnassa. Lisäksi tutkin, vaikuttaako aikaisempi kokemus siihen, mitä marjanväriä lintu suosii vertailemalla luonnosta pyydettyjen aikuisten ja käsinkasvatettujen nuorten lintujen välisiä eroja. Tutkimusteni perusteella aikuiset linnut suosivat UV-valoa heijastavia marjoja enemmän kuin mustia tai punaisia marjoja. Tähän vaikuttaa myös valaistusolosuhteet; jos UV-valoa ei ole käytettävissä, linnut syövät mustia ja sinisiä mustikoita yhtä paljon. Taustan väri ei vaikuttanut siihen, syövätkö linnut enemmän punaisia vai UV-sinisiä marjoja. Nuoret linnut eivät suosineet mitään marjanväriä, tosin ne söivät vähiten valkoisia marjoja. Nuoret linnut söivät kuitenkin UV-sinisiä marjoja enemmän kuin punaisia UV-siniseltä taustalta, mutta söivät sekä UV-sinisiä että punaisia marjoja yhtä paljon punaiselta ja vihreältä taustalta. Kun käytin keinotekoisia UV-valoa heijastavia ja absorboivia signaaleja ravinnon yhteydessä, aikuiset ja nuoret linnut eivät suosineet kumpaakaan signaalia, tosin yksilölliset erot olivat suuria. Kun opetin niitä suosimaan alussa vähemmän suosimaansa signaalia, lintujen valinnat muuttuivat.

Väitöskirjatyöni tulosten perusteella voidaan olettaa, että luonnonvaraiset linnut todennäköisesti oppivat suosimaan tiettyjä marjanvärejä. Jos linnut synnynnäisesti suosivat tai välttivät jotain väriä, tämä taipumus voi muuttua kokemuksen myötä. Taustaväriin kontrasti marjanvärin kanssa saattaa toimia pidemmältä etäisyydeltä kuin mitä kokeessani käytettiin. Värikontrasti saattaa kiinnittää ravintoa etsivien, lentävien lintujen huomion tehokkaimmin luonnonolosuhteissa.

Viimeisessä osatyössäni tutkin, eroaako lintujen suoliston läpi kulkeutuneiden siementen itämiskyky suoraan mustikoista kerätyistä siemenistä. Lintujen ruuansulatuselimistön vaikutusta eri kasvilajien siementen itämiskykyyn on tutkittu melko paljon; itävyys voi parantua, pysyä muuttumattomana tai heikentyä. Eri lintulajien vaikutus saman kasvilajin siementen itävyyteen voi myös vaihdella. Kuitenkaan siementen keruuajankohdan mahdollista vaikutusta näiden tutkimusten tuloksiin ei ole tutkittu. Jos siementen itämisominaisuudet, esim. dormanssin syvyys, muuttuvat kasvukauden aikana tai vaihtelevat vuosittain, tämä voi vaikuttaa tutkimustuloksiin. Tässä osatyössä olen tarkastellut myös keruuajankohdan vaikutusta itävyyteen. Suoraan marjoista kerättyjen siementen itämisnopeus hidastui kasvukauden edetessä. Nopeimmin itivät pian marjojen kypsyttyä kerätyt siemenet. Lintujen läpi kulkeutuneiden siementen itävyys ei hidastunut yhtä paljon. Rastaiden suoliston läpi kulkeutuneet siemenet siis itivät nopeammin, ja lisäksi niiden kokonaisitävyys oli yhtenä vuotena parempi ja toisena vuotena yhtä suuri kuin suoraan marjoista kerättyjen siementen. Nämä tutkimustulokset osoittavat, että tutkittaessa hedelmänsyöjien vaikutusta hedelmäkasvien siementen itävyyteen, aineistoa tulisi kerätä useana eri kasvukauden ajankohtana sekä eri vuosina. Siementen keruuajan kohta ja -vuosi saattavat merkittävästi vaikuttaa tuloksiin ja niiden tulkintaan.

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