

Heli Siitari

Ultraviolet Sensitivity in Birds:
Consequences on Foraging
and Mate Choice



UNIVERSITY OF JYVÄSKYLÄ

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*To my lovely daughters,
Sara and Sanna*

ABSTRACT

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Ultraviolet sensitivity in birds: consequences on foraging and mate choice

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Yhteenveto: Lintujen ultraviolettinäön ekologinen merkitys ravinnon- ja puolisonvalinnassa

Diss.

In addition to human-visible waveband (400-700 nm) birds are sensitive to near ultraviolet (UV) waveband (UV-A; 320-400 nm). The aim of this thesis was to contribute to the understanding of importance of UV sensitivity in foraging and mate choice in birds. First I conducted two separate laboratory experiments with redwings (*Turdus iliacus*) and with black grouse (*Tetrao tetrix*) to test whether UV wavelengths are used when birds are feeding on bilberries (*Vaccinium myrtillus*). The colour preferences of birds varied due to different UV light levels in the light environment. Both experiments show that UV may be a good advertisement colour in light environments rich in short wavelength light. In the other three papers I investigated the importance of UV cues in intraspecies signalling in pied flycatchers (*Ficedula hypoleuca*) and in blue tits (*Parus caeruleus*). According to the field study, adults had higher UV reflectance levels than yearlings, and males had higher UV reflectance levels than females. Proportional UV reflectance of dorsal side of pied flycatchers was negatively related to male arrival time to the breeding sites. This was independent of male brownness. Thus, UV reflectance of plumage may be related to male quality in pied flycatchers. The results of the outdoor aviary mate choice experiment suggest that females use UV cues of plumage when choosing mates, at least when males are displaying simultaneously and the territory quality is controlled for. In the last study I did not find any strong relationship between human-invisible colour and parental quality. However, long-time field studies are needed to investigate this relationship. The results of this thesis show that birds can detect UV cues of light environment and UV cues of plumage. Therefore, the UV sensitivity of birds should be taken into account especially when studying plumage colours and conducting colour manipulations and conducting experiments in artificial light conditions.

Key words: *Ficedula hypoleuca*; foraging; mate choice; mate quality; *Parus caeruleus*; sexual selection; *Tetrao tetrix*; *Turdus iliacus*; ultraviolet.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles which are referred to in the text by their Roman numerals. I have personally written each paper and performed and planned large part of the work.

- I 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*). Proceedings of the Royal Society London B 266: 2125-2129.
- II Siitari, H., Hovi, M. & Viitala, J. 2001. Behavioural evidence on ultraviolet vision in a tetraonid species –a foraging experiment with black grouse (*Tetrao tetrix*). Submitted.
- III Siitari, H. & Huhta, E. 2001. Individual colour variation and male quality in pied flycatchers (*Ficedula hypoleuca*). Submitted.
- IV Siitari, H., Honkavaara, J., Huhta, E. & Viitala, J. 2001. Ultraviolet reflection and female mate choice in the pied flycatcher (*Ficedula hypoleuca*). Initially accepted (Animal Behaviour).
- V Siitari, H. 2001. Colour variation and reproductive success in pied flycatchers and blue tits. Manuscript.

1 INTRODUCTION

1.1 Ultraviolet sensitivity in birds

1.1.1 Bird vision vs. human vision

Much of the research on bird behaviour is at least to some degree connected to vision. Birds rely on their vision in many daily routines, like foraging and mate choice. Indeed, vision may be the most important sense what comes to birds.

It is important to notice that bird vision, especially colour vision, differs considerably from that of humans. Our own colour vision is poorly developed compared to colour vision of most other vertebrates. Nevertheless, the human colour vision is better than the colour vision of most other mammals; most mammals have only two types of retinal cones and consequently, only dichromatic colour vision in contrast to three types of retinal cones and trichromatic colour vision in humans (Jacobs 1981). Most birds, however, have four types of retinal cone photoreceptors and thus, tetrachromatic colour vision (Bowmaker et al. 1999). This also means that birds have four classes of cone visual pigments – a long wavelength sensitive (LWS), a medium wavelength sensitive (MWS), a short wavelength sensitive (SWS), and an extreme short wavelength sensitive (UVS/VS) “UV” or “violet” pigment (Cuthill et al. 2000 and references therein). Thus, many birds are sensitive also to near ultraviolet (UV) wavelengths. However, birds are sensitive to (UV) wavelengths primary because their ocular media (particularly lens and cornea) are UV transparent. Actually, all vertebrates have the potential for UV vision unless short wavelengths are specifically absorbed before reaching the retina (Cuthill et al. 2000). For example, in addition to the lack of UV sensitive type of pigment in the retina, humans have UV absorbing pigments in the lens of the eye, which primary omits the UV sensitivity (Goldsmith 1991).

In addition to four types of visual cones and UV sensitivity, birds have oil droplets with a special function in their eyes. Light is achieved via coloured oil droplets, which lie within the cone cells. Their function is to filter the light

coming to certain cone by cutting out wavelengths somewhat less than the λ_{\max} of the visual pigment (e.g. Goldsmith et al. 1984, Hart et al. 1998).

1.1.2 Function of ultraviolet vision in birds

The sensitivity of birds to UV light was first demonstrated in 1972 in hummingbirds (Huth & Burkhardt 1972) and in pigeons (Wright 1972). Birds possibly use UV cues that are undetectable to humans, for example in mate choice and foraging. This has inspired researchers, mainly from 1990's onwards, to carry out behavioural experiments. So far, we know that birds can use UV cues at least in mate choice and foraging. For example, many birds have UV reflecting characters in their plumage (Burkhardt 1989, Burkhardt & Finger 1991, Maier 1993, Bennett & Cuthill 1994, Finger & Burkhardt 1994, Andersson 1996, Bennett et al. 1996, 1997, Andersson & Amundsen 1997, Andersson et al. 1998, Hunt et al. 1998, Cuthill et al. 1999, Keyser & Hill 1999). Maier (1993) was the first to show in a behavioural test that Pekin robins (*Leiothrix lutea*) preferred partners that were viewed through a UV-transmitting filter to those that were viewed through UV-blocking filters. Bennett et al. (1996) reported the similar effect in zebra finches (*Taeniopygia guttata*). Female starlings (*Sturnus vulgaris*) ranked the males in a consistent manner in illumination that included UV light; preference was correlated with the UV reflectance of iridescent feathers of the throat (Bennett et al. 1997). However, when UV light was blocked they did not find any correlation between male rank and plumage reflectance (Bennett et al. 1997). Starlings also exhibit sexual dimorphism in UV coloration (Cuthill et al. 1999), as does the blue tit (*Parus caeruleus*; Andersson et al. 1998, Hunt et al. 1998).

UV cues may be of highest importance in species with pure UV reflecting ornaments. An example of this is the UV/blue coloration of the crown in the blue tit. Blue tits are sexually dimorphic in colour, and the difference in coloration between the sexes is greatest in the UV waveband (Andersson et al. 1998, Hunt et al. 1998). Thus, both females and males appear quite similar to the human eye. Females prefer males with the brightest crowns (Hunt et al. 1998), and in the field Andersson and co-workers found assortative mating based on the UV chroma (a measure of saturation) of crown (Andersson et al. 1998). In a laboratory experiment, Hunt et al. (1999) found that blue tit males also associated more with females having the brightest crown coloration. Furthermore, Sheldon et al. (1999) found that female blue tits adjusted the sex ratio of their brood based on the UV coloration of males. The sex ratio was male-biased in broods of females mated to males with unmanipulated UV chromas compared to the broods of females mated to males of which UV chroma was experimentally reduced. Moreover, UV chroma predicted male survival to the next breeding season (Sheldon *et al.* 1999). In addition to blue tits, UV cues affect both social and extra-pair mate choice in bluethroats (*Luscinia svecica*) (Andersson & Amundsen 1997, Johnsen et al. 1998), and function as an honest signal of male quality in the blue grosbeak (*Guiraca carulea*) (Keyser & Hill 1999, 2000).

The ecological importance of UV vision in foraging has received less attention as compared to the study of sexual selection. Viitala et al. (1995) were the first to show that wild birds use UV wavelengths when foraging. Scent marks of small rodents are known to be visible in UV light due to fluorescence (Derjardins et al. 1973), as the scent markings absorb part of UV radiation and emit the absorbed energy as visible light. A totally new finding was that scent marks have a special hue visible only in UV light. In the laboratory study Viitala et al. (1995) found that European kestrels (*Falco tinnunculus*) use the scent marks of voles as a cue of prey. This was also demonstrated in a large-scale field experiment (Viitala et al. 1995), in which raptors spent more time hunting above areas treated with vole scent marks compared to control areas treated with water. The visibility of scent marks in UV light differs between vole species and also between reproductive categories of voles, and kestrels may be able to distinguish these categories (Koivula 1998, Koivula et al. 1999a, Koivula et al. 1999b). Recently, it has been found that rough-legged buzzards (*Buteo lagopus*, Koivula & Viitala 1999) and great grey shrike (*Lanius excubitor*, Probst et al. unpublished 2001) use UV cues of voles when foraging. However, Tengmalm's owls (*Aegolius funereus*) did not respond to the UV cues of prey (Koivula et al. 1997), supporting the hypothesis that nocturnal owls lack the cones sensitive to UV light (Bowmaker & Martin 1978).

Birds can also use UV cues when searching for invertebrate prey. However, it is unknown whether birds utilise these UV patterns in prey detection or recognition (Cuthill et al. 2000). Church et al. (1998a) investigated the foraging behaviour of blue tits in a laboratory arena using cryptic insect prey as a prey object. They manipulated the light environment using UV transmitting and UV blocking filters and investigated how it affects prey detection. The latency to find the first prey item increased in trials in which UV was blocked with the filter. This may be because prey detection can be lowered due to a reduction in perceived brightness, and the hue of both prey and background may render the task more difficult (Church et al. 1998a). However, if the spectral reflectance of prey and its background differs in the UV part of the light spectrum, prey may be highly detectable in UV light to UV sensitive predators. There are at least some caterpillars that are cryptic in visible light but reflect the light in the UV waveband (Church et al. 1998b), indicating aposematic coloration and possibly advertising their unpalatability and/or poisonousness (Church et al. 1998b). However, Lyytinen et al. (2001) found that UV cues alone neither signal unpalatability nor work effectively as aposematic signals to great tits (*Parus major*).

1.2 Aim of the thesis

The aim of my work is to contribute to the understanding of the importance of UV cues in foraging and in intraspecies signalling in birds.

In the first two papers I examined the colour preferences of redwings (*Turdus iliacus*) (I) and black grouse (*Tetrao tetrix*) (II) in the presence and

absence of UV light manipulating the UV light levels. In the third paper I investigated the individual colour variation, sex and age differences and quality (in terms of arrival time to the breeding site) in the field in pied flycatchers (*Ficedula hypoleuca*), exploring the determination of colour to the little studied UV waveband of light (III). In paper four, I tested the effect of manipulation of UV waveband of males' plumage on female mate preferences in pied flycatchers (IV). In the fifth paper, I examined the effect of colour, especially UV coloration, on reproductive success in both pied flycatchers and blue tits (V).

2 MATERIALS AND METHODS

2.1 The species

I have studied the importance of UV cues in several species. In the first paper (foraging experiment) I used redwings (*Turdus iliacus*), which are abundant passerine birds nesting in Finland. Pairs typically have one to two broods per summer. In summer time, their diet consists mainly of insects and their larvae, but in autumn, berries (especially red currant (*Ribes rubrum*) and bilberry (*Vaccinium myrtillus*), are also important. The possibility of UV sensitivity in redwings is not physiologically investigated, but earlier study with another *Turdus*-species revealed UV sensitivity in blackbirds (*Turdus merula*, Hart et al. 2000). In the experiment, I used both experienced adult and naïve young-of-the-year redwings. To get naïve birds to the experiment, we hand-raised the broods at the Konnevesi Research Station in summer 1998. Parents from nest sites were mist-netted at the same time and taken to the laboratory.

In the second paper (foraging experiment) I investigated the colour preferences and UV sensitivity in a galliform species, the black grouse (*Tetrao tetrix*). In addition to capercaillie (*Tetrao urogallus*), the black grouse is the other tetraonid species living in Finland. The main summer diet of adult tetraonid species consists of green leaves and buds, but berries (e.g bilberry, bog bilberry (*Vaccinium uliginosum*)) are an important source of food especially in autumns due to their high sugar contents. The UV sensitivity of black grouse is unknown, but other galliform species studied have potential for UV sensitivity (*Coturnix coturnix japonica*, Bowmaker et al. 1993; *Gallus gallus domesticus*, Bowmaker et al. 1997; *Meleagris gallopavo* and *Pavo cristatus*, Hart N.S. 1998 PhD-thesis, reference in Cuthill et al. 2000).

In the other papers (III, IV, V) I used pied flycatchers (*Ficedula hypoleuca*) as model species. Pied flycatcher is a small (12-13 g) migratory passerine of northern and central Europe. It prefers nest-boxes to natural cavities as breeding sites, and has only one brood per summer. The species is one of the most studied bird species in the world, and thus, the ecology is well-known

(Lundberg & Alatalo 1992). Pied flycatchers overwinter in West Africa. In spring, the first males arrive to study sites (Konnevesi, Central Finland) in early May about a week ahead of the first females. Males establish a territory and start singing to attract females. The territory quality is believed to be the most important cue in female mate choice. Some of the males become polyterritorial and polygynous. The UV sensitivity is unknown, but like other passerines studied so far, it potentially has tetrachromatic colour vision with UV sensitivity.

In the study V, in addition to pied flycatchers, I used also blue tits as the other model species. Blue tit is a mostly monogamous bird species. Sexes look similar to the human eye, but sexual dimorphism in crown coloration, especially in the near UV waveband, has been found (Andersson et al. 1998, Hunt et al. 1998). The UV coloration of crown affects female mate preferences (Hunt et al. 1998), and assortative mating according to crown UV chroma (a measure of saturation; see section 2.2 Spectroradiometry for details) has been found (Andersson *et al.* 1998). Pairs typically have one brood per summer. The eye physiology has been investigated, and blue tits have UV sensitive cone cells in their retina (Hart et al. 2000).

2.2 Spectroradiometry (I, II, III, IV, V)

When studying colour patterns of animals, it is important to know how the colour of objects appears to the observer. At least four factors are involved with the appearance of an object (Silberglied 1979):

1. *The light environment.* The spectral quality and intensity of light varies over time and space.
2. *The optical property of natural objects.* Light is reflected, absorbed and transmitted by matter. The spectral quality and intensity of reflected and transmitted light carries information about matter to the eye.
3. *The visual system.* Light is refracted, filtered and absorbed in the eye. The optical properties of the eye and spectral absorption of receptor pigments determine what information will be transduced to electrical signals.
4. *The brain.* The appearance of the world to the organism depends upon how the brain interprets the spatial and chromatic information sent to it by the visual receptors.

If the visual system of the study object is different from the observer, it is necessary to find a way to determine colours objectively. I carried out the colour measurements (papers I, II, III, IV, V) with a spectroradiometer (EG & G Gammascientific GS 3100). I measured the reflectance spectra over the bird visible spectrum (320-700 nm). As a light source I used EG & G RS-22 UV xenon fibre optic light source that is effective enough also in the near UV (UV-A) waveband. The light source was connected with a probe to an adjustable stand (hand-made stand in papers I, II, and in paper III when measurements were

carried out in 1995, and a Gamma Scientific 191C-02 stand in paper III (the measurements carried out in 1999), IV and V). When measuring the spectrum the measuring object was illuminated at the angle of 45° by the light source. Reflected light was collected with the fibre optic probe at 90° connected to a mounting stand in a fixed distance. Each spectrum was measured in 5 nm intervals and measured in relation to a calibrated 98% reflectance standard (LabSphere™). When measuring the spectrum, it is important that the lighting and measuring angles are constant during all the measurements. This is because the angle greatly affects the spectrum measured, particularly when measuring colours based on structural components (like most UV colours; Simon 1971, Endler 1990, Cuthill et al. 2000). However, if the angle is constant, the measurements are comparable to each other.

Humans perceive and classify colours mainly using three properties: brightness, hue and chroma (Endler 1990). Brightness clearly depends on viewing conditions. For example, if the ambient light spectra is rich in middle (meaning green and yellow) wavelengths, so patches which reflect most strongly in these wavelengths will be brighter than other patches. However, hue and chroma are associated with the physical properties of light (Endler 1990). Hue is defined as 'colour', e.g. violet, green, red etc. In the spectrum measured, hue is a function of its shape, meaning the maximum slope of the spectrum. Some colours are not monotonic and have two maximum slopes, e.g. the yellow breast pattern of great tits (Hunt et al. 1998). Chroma is a measure of the 'purity' or 'saturation' of a colour (Endler 1990). It describes the function of how rapidly intensity changes with wavelength.

When comparing colour variation among individuals in papers III-V, I used UV chroma values as a measure of colour (referred as relative UV reflectance; describing the saturation of UV in each spectrum). It was calculated as a proportion of reflected UV light of total light reflected in each spectrum, using the following formula

$$\text{UV chroma} = R_{(320-400\text{nm})} / R_{(320-700\text{nm})}$$

2.3 Laboratory experiments (I, II)

In the first and second paper I examined how altering of light conditions affects colour preferences of redwings (I) and the black grouse (II). My aim was to test whether redwings (I) and black grouse (II) prefer UV reflective bilberries over black ones. It is suggested that the UV reflective wax layer of fleshy fruits could serve as an effective advertisement for frugivorous birds (Burkhardt 1982) informing both visibility and quality of the berries. Thus, UV sensitive birds could use UV reflectance of fruits as a foraging cue. I tested the birds in two separate light conditions (high and low UV levels; referred to as UV+ and UV-conditions, respectively) using UV reflective and black bilberries, and investigated whether preferences were altered due to different light conditions. I manipulated UV levels using either UV transmitting or UV blocking filters

and a constant light source (Osram Eversun L 40W/79K solarium tube and Osram Biolux L 18W/72; paper I), or manipulating UV levels of light environment by changing light source (Philips MLW 160W in UV+ conditions, Philips 60W in UV- conditions; paper II). In the first paper I used the normal waxy UV colour morph of bilberries, but rubbed the wax from half of the berries to get black berries of similar taste. In contrast to the first paper, in the second paper I used two separate colour morphs of bilberry, natural, and more common UV reflective bilberry and black colour morph of bilberry, which lack the wax layer and appear black to the human eye. Birds were tested either once in UV+ and UV- light conditions (I) or 2-4 times in both light conditions, respectively (II). In the first experiment (I) I used both experienced (familiar with berries) adult and naïve, hand-raised young-of-the year redwings. In the second experiment all the birds were captive-born black grouse, but they were fed occasionally with bilberries.

2.4 Field studies (III, IV)

2.4.1 The study area and populations

In the field studies (III, V) I examined the relationship between colour (including that measured in the UV waveband from 320 to 400 nm), individual quality, age and sex (III) and relationship between colour and parental quality using several reproduction success parameters (V). As model species I used pied flycatchers (papers III and V) and blue tits (V). The data for papers III and V have been collected from nest-box populations breeding in Konnevesi region (62°37'N, 26°20'E) during the years 1995, 1999 and 2000. The nest-box areas are mainly in coniferous forests dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) or their mixture. In total, there are 250 nest-boxes in the study area available for pied flycatchers and blue tits.

2.4.2 Colour variation, age and sex differences and relationship to male quality (III)

In paper III, I used male arrival time to the breeding sites as a measure of male quality. First arriving males gain the best territories, and in pied flycatchers, territory quality is an important cue in female mate choice (Alatalo et al. 1986). Moreover, in polyterritorial and polygynous species early arrival improves the male's possibilities to gain a secondary territory and chances to mate polygynously (Alatalo et al. 1984, 1990). The nest box areas were visited daily in May to assess males' arrival times (III). Pied flycatcher males are easy to detect, because immediately after territory establishment they start to advertise their territory by singing. After detection of each new male, it was captured using nest-box traps and taken to the laboratory for spectroradiometric measurements (see chapter 2.2). The spectra were measured from crown, back and breast. Each region was measured twice changing the place of measurement spot between

the scans. I calculated the relative UV reflectance (UV chroma) from plumage reflectance spectra (see chapter 2.2 Spectroradiometry) which was used to describe the proportional UV reflectance in each body region. I then calculated the average between the UV chroma values of two measurements. The reflectance spectra of crown and head were combined to one variable, dorsal side, by calculating the average of mean UV chroma values of crown and back. Male plumage colour (brownness) was also scored by human eye from 0 to 100. A score of 0 means a male with totally black dorsal side, and a score of 100 totally female-like male with light brown dorsal side. Males were also ringed with aluminium bands and aged either adults or yearlings on the basis of the colour and shape of outer wing coverts (Lundberg & Alatalo 1992). After the procedures the birds were released back to their territories. Females were also caught during incubation for colour measurements, and ringed, aged and taken back to their nests.

2.4.3 Colour and parental quality (V)

To study how colour might be related to the quality of parents I conducted a field study on pied flycatchers and blue tits (V). As parameters of reproductive success, I used timing of breeding, number of eggs laid (clutch size), fledging success (number of fledged young in a nest) and mean fledging weight.

As a timing of breeding, I used the day of initiation of egg laying. The initiation of egg laying in both species was observed by visiting nest-boxes regularly. If necessary, the clutch initiation date was calculated regressively assuming that one egg per day was laid.

Clutch size was determined by visiting nests regularly after initiation of egg laying until the clutch was completed. After the clutches were completed, I inspected them daily around the estimated hatching day until the first egg hatched. The estimated hatching time in both pied flycatchers and blue tits is about 13-16 days after the clutch is completed.

When the chicks were 8-9 days old, I captured both parents for colour determination, which occurred at the research station using the spectroradiometer. I also measured the tarsus length, weight and determined age from each bird and scored the human-visible colour from pied flycatcher males.

Fledging of young occurs normally when the chicks are 15-16 (pied flycatcher) or 18-20 (blue tit) days old. However, chicks can leave the nest before that age in case of any disturbance. Thus, the number of young in a day 13 in a nest was used as a measure of fledging success. However, nests of blue tits were checked after fledging date to check for any dead young, so that the number of fledged offspring could be correctly counted. I also weighed the chicks in a day 13, which is comparable to the fledging mass. This is because the mass of chicks remains quite constant after day 12 (Lundberg & Alatalo 1992). Furthermore, mass of 13-d nestlings is strongly related to post-fledging survival in many passerine birds (Perrins 1965, Nur 1984, Linden et al. 1992, Lundberg & Alatalo 1992). However, also contrary results in the blue tit population in Gotland exist (Merilä et al. 1999).

For the analysis, I calculated the proportional UV reflectance for each spectrum. To take into account the effect of human-visible colour in blue tits, I also calculated the saturation between 320 and 420 nm in relation to total reflectance from 320 to 700 nm. This is because the peak of the reflectance spectrum is in the human visible area, around 420 nm (Andersson et al. 1998, Hunt et al. 1998).

2.5 Outdoor aviary experiment (IV)

To investigate how altering of plumage UV reflectance levels affects female mate choice preferences in pied flycatchers, I conducted an outdoor aviary experiment. In the aviary ($3 \times 3 \times 2 \text{ m}^3$) females could choose between two simultaneously displaying males, and female nest building was used as a criterion for her choice. Males were situated in separate compartments, each having the two-part nest box separated with a nylon net from female's part of nest box and female compartment. The similar system has been used in many mate choice experiments in Norway (e.g. Saetre et al. 1994, Saetre et al. 1997, Slagsvold & Viljugrein 1999).

For the experiment I manipulated the relative UV reflectance of the dorsal side in pied flycatcher males. The relative UV reflectance (UV chroma) before the manipulation, visible brownness, weight and tarsus length did not differ between males in pairs. To reduce the relative UV reflectance, I mixed sunscreen (Nivea 15) with a control substance (fly dressing, Ultrafloat) in proportion of 3:1, and greased the dorsal side of male with the mixture. The other male was also treated but only with the control substance. The sunscreen reduces the UV component effectively but affects the reflectance in human-visible waveband only slightly. However, due to gloss of the control substance the total reflectance and the UV chroma increased slightly in control males.

Males were released to the aviary about 4-8 hours before the female was introduced. In addition to female choice, the male display behaviour (enticement calls, visits to nest box) was observed in nine out of 13 successful trials.

3 RESULTS AND DISCUSSION

3.1 UV vision in foraging (I, II)

The results suggest that the UV reflective wax layer of berries may be a good advertisement colour for fruit-eating birds. In UV+ light conditions both redwings (I) and the black grouse (II) preferred UV reflecting berries to black ones. However, they did not prefer either berry colour type (UV reflective vs. rubbed black berry in paper I; UV reflective vs. natural black colour morph in paper II) if the UV level of light environment was reduced either blocking the emitting UV light by filters (I) or by using an ordinary bulb instead of a UV lamp as a light source (II). The birds, however, did not unequivocally avoid the UV reflecting berries in UV- conditions, which may prove that berries of this colour did not appear odd in bird's eye view.

However, in the first paper naïve, hand-raised birds used in the experiment did not show any absolute preferences to UV reflective or black berries. This might be due to a difference in sensory capacity between adult and young birds, but it does not exclude the possibility that young birds could not detect UV light. The lack of preference could be explained, for example by the sampling behaviour of the naïve birds. This is because most of the naïve birds also chose the UV reflecting berry first, but after the first choice the choice was more or less random. Young birds may also learn, e.g. by mimicking adults (i.e. by social learning) what is suitable and preferred for food.

UV may be an effective advertisement colour in certain light habitats. Bilberries grow predominantly in habitats similar to woodland shade (classification in Endler 1993). This light environment is rich in short wavelength light. Therefore to maximise their brightness, signal colours should be blue, green or perhaps ultraviolet (Endler 1993). In these light conditions the UV reflective wax layer might be a good advertisement for seed dispersers that are sensitive to UV light. Moreover, we have shown that berry ingestion by birds enhance seed germination success and speed up germination compared to seeds without bird ingestion (Honkavaara, Siitari, Saloranta & Viitala,

unpublished manuscript). Thus, interaction between birds and bilberries benefits both plant and bird.

3.2 UV vision, male quality, age and sex differences (III)

Pied flycatcher males with higher proportional UV reflectance in their dorsal side arrived earlier to the breeding sites. This was independent of male brownness (scored by human eye) meaning that also brown males arriving early had proportionally more UV reflectance than later arriving black males. The relative UV reflection of white breast was negatively related to male brownness. This indicates that black males had proportionally more UV reflection than brown males in their breast increasing the contrast between white breast and dark dorsal side in black males. Age also affected the coloration in human visible waveband: older males were darker than young ones. However, when comparing proportional UV reflectance of adult and yearling males to females (which are totally brown when scored with human eye), adult males had proportionally higher UV chroma values in the breast than yearling males and females, but females and yearling males did not differ from each other. Females had lower proportional UV reflection in the dorsal side, compared to both adult males and yearling males, but the UV chroma of the dorsal side of males of different age classes did not differ.

According to the results, the proportional UV reflectance of plumage, particularly the UV reflection of the dorsal side might be related to male quality in pied flycatchers. This is because UV reflection of dorsal side was strongly negatively correlated with the arrival time to the breeding sites. Only males in good condition are able to arrive early and tolerate the costs associated with the early arrival (Alatalo et al. 1984, Møller 1994a & b, Kokko 1999). Thus, the relative UV reflection of the dorsal side might be condition-dependent.

The results support the two recent studies in which researchers have found condition-dependent variation in structural based UV coloration in blue tits (*Parus caeruleus*, Sheldon et al. 1999) and in blue grosbeaks (*Guiraca caerulea*, Keyser & Hill 1999). Blue tit males that had survived the winter had higher UV chroma values in the crown than males that were not recaptured (Sheldon et al. 1999). Moreover, reduction of UV reflectance of crown affected brood sex ratios; males with greater UV reflection in the crowns had proportionally more sons in their broods than males with experimentally reduced UV reflection (Sheldon et al. 1999). In blue grosbeaks, expression of blueness in plumage is positively correlated to increased tail feather growth (Keyser & Hill 1999), and intensity and size of the blue/UV ornament is positively related to male body size, territory size and prey abundance in the same species (Keyser & Hill 2000). However, the colour of pied flycatchers is melanin based (Lundberg & Alatalo 1992). Although melanin based colours are not expected to reflect UV light (Burkhardt 1989), variation in the UV reflectance has been indicated (Burkhardt 1994, Hunt et al. 1998). However, many structural colours are produced by melanin in layers, e.g. the structural-based UV reflecting colour of starling

plumage (Bennett et al. 1997). The melanin production, especially producing melanin in layers may be more costly than previously expected, and the costs of structural-based ornaments are unknown.

3.3 UV vision and female mate choice (IV)

Females preferred the male with non-reduced relative UV reflectance in 11 out of 13 successful trials. The only trait that differed between accepted and rejected males was the relative UV reflectance of the dorsal side. Thus, male display behaviour or date of trial did not affect the results.

This experiment shows that the relative UV reflectance of males affects female mate choice decisions at least in the situation when males are displaying simultaneously and territory quality is controlled for. In the field, as shown in paper III, males with higher proportional UV reflectance in their plumage arrived first to the breeding sites and probably will get the best territories. On the other hand, early arriving females, when preferring the males with high territory quality may similarly get the males of the better quality. This may assure both genetic and environmental benefits to the offspring. UV cues of males may also play a role when females are seeking extra-pair mates, especially if UV cues are related to mate quality.

Previous work on mate choice in this species has concentrated on comparing female preferences of males that differ in human-visible brownness (Alatalo et al. 1990, Saetre et al. 1994, Saetre et al. 1997), and results are divergent. However, according to paper III, human-visible brownness itself may be a poor indicator of male quality. It is predictable that UV might be a special communication channel in species with pure UV ornaments (like in blue tits and blue grosbeaks), like the long wavelength band e.g. in zebra finches. In zebra finches red bill coloration of males varies and is preferred by females (e.g. Burley & Coopersmith 1987). Removal of UV cues using UV blocking filters affected negatively female mate choice in this species (Bennett et al. 1996), but removal of red cues had even greater effects on female mate preferences (Hunt et al. 2001). The question whether the UV waveband is somehow a special channel in communication in pied flycatchers remains unanswered. At least, there is variation in the plumage colour in the UV waveband that might be related to individual quality (III), and the UV cues affect female mate choice decisions. Furthermore, our sunscreen manipulation did not remove all the UV reflection but reduced relative UV reflectance effectively.

3.4 Colour and reproductive success (V)

According to my field study, colour, and particularly the human-invisible part of the light spectrum, does not indicate parental quality in pied flycatchers or blue tits. This is at least what comes to reproductive success parameters I have used in my study (timing of breeding, clutch size, number of fledged young and mean fledging mass of young). However, due to poor weather conditions the data remained too small, and the erratic effect of environment was even greater than in normal summer weather conditions. Some 39% of pied flycatcher nests and 41% of blue tit nests failed during the observation season.

The results support the hypothesis that in territorial species (especially in pied flycatchers) the territory quality may affect reproductive success even more than mate characteristics. However, it is quite difficult to separate the effects of territory quality and mate characteristics. This is because males in the best condition may be able to obtain the best territories and thus, both male and territory quality may affect male reproductive success.

I did not find that crown coloration of males would have affected male reproductive success parameters in blue tits. It may be also that females will obtain indirect genetic benefits when choosing males with elaborate ornaments (such as colour in blue tits). In previous work Kempenaers (1997) indicated that females preferred males that had survived the winter when seeking partners for extra-pair matings. In this way, females may try to improve the genetic quality of their offspring. Recently, Sheldon et al. (1999) showed that males with higher proportional crown UV reflectance survived the winter better than males with lower UV reflectance. Furthermore, in breeding season 2000 the weather conditions varied greatly, which might have affected the parents' ability to feed the nestlings and thus, potentially affected negatively the growth rate and survival of nestlings. This effect of erratic weather conditions might have had strong effects upon the results of this study, and my plan is to conduct further studies in following years.

4 CONCLUSIONS

Although UV vision in birds was first demonstrated in the early 1970s', it has been investigated in more detail only from the 1990s' onwards. However, it is important to notice the difference in the whole sensory capacity, not only in vision, when studying and trying to understand the evolution of organisms that differ in their way to observe the world compared to humans.

In this thesis I studied various questions about colour signalling, especially the importance of UV cues invisible to humans, and how certain birds species are able to distinguish these 'hidden' cues. In papers I and II (foraging experiments) I found that food colour preferences of both redwings and black grouse varied due to altering light conditions (normal or reduced UV light levels in the light environment). This experiment indicates that both species are able to detect UV light. Furthermore, it indicates that UV cues may be more effective in certain light conditions, which may have affected the evolution of e.g. fruit colours.

In the previous papers I investigated the importance of UV cues of birds' plumage. I found that UV cues might indicate male condition in pied flycatchers (III). There were also sex (III, V) and age (III) differences in UV reflectance in different parts of plumage, females and younger males having lower UV reflectance levels than adult males. Manipulation of UV cues of males also affected female mate preferences: females clearly preferred males with non-reduced UV cues (IV). In the last paper (V) I investigated the relationship between colour and parental quality. However, I found no effect of colour (UV or human-visible coloration) on reproductive success parameters in pied flycatchers (V). This indicates that in nature, territory quality and other environmental factors may affect reproduction success more than male/female characteristics. Previously, in blue tits colour of crown has been shown to affect both female and male mate choice decisions (Andersson et al. 1998, Hunt et al. 1998, Hunt et al. 1999). Thus, colour cues may also potentially indicate parental quality, at least in some species. On the other hand, male quality (in terms of reproductive success parameters and timing of breeding) did not seem to

correlate with the crown coloration in blue tits in my study. However, the indirect effects of female choice remain unstudied. Moreover, blue tit females possibly could improve the quality of offspring through extra-pair copulations. In this species, females seem to prefer the males that had survived the winter when seeking extra-pair matings. In a recent study the UV chroma of crown was positively related to male survival (Sheldon et al. 1999), which supports the hypothesis on relationship between colour and male quality in blue tits.

To conclude, UV cues that are invisible to humans affect the behaviour of birds. UV cues of light environment affect colour preferences of redwings (Siitari et al. 1999), and also a tetraonid species, the black grouse, use UV cues when foraging. UV cues of plumage are potentially related to sex (Andersson et al. 1998, Cuthill et al. 2000, Siitari & Huhta manuscript 2001) and age (Andersson & Amundsen 1997, Siitari & Huhta manuscript 2001). UV cues of plumage may also indicate male quality (Keyser & Hill 1999, 2000, Sheldon et al. 1999, Siitari & Huhta manuscript 2001) and affect female mate choice decisions in pied flycatchers at least if the effect of territory quality is controlled for (Siitari, Honkavaara, Huhta & Viitala initially accepted manuscript 2001). However, colour seems not to have major effects on reproductive success of females and/or males in terms of parental quality, or at least the effects are weak in harsh and erratic environmental conditions (Siitari 2001, manuscript).

The difference in colour vision between humans and birds should be taken into account, especially when studying colours. This is not only what comes to UV waveband, but other colours, too. UV ornaments may not be more special than other ornaments, but their importance has been unknown so far, due to our physiological handicap. Special care should be exercised when conducting experiments with artificial objects and when conducting colour manipulations and experiments in artificial light conditions. Conversely, if colour is measured objectively, this offers a new and interesting way to investigate several questions in evolution and behavioural ecology.

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YHTEENVETO

Näköaisti on kaikista eläimistä ehkä tärkein juuri linnuille. Linnut luottavat monissa toiminnoissaan, kuten esimerkiksi ravinnonvalinnassa ja keskinäisessä signaloinnissaan, näköaistiinsa. Lintujen näkemä värimaailma kuitenkin poikkeaa ihmisten näkemästä värimaailmasta. Ihmisilmä pystyy havaitsemaan elektromagneettista säteilyä (valoa) aallonpituusvälillä 400-700 nm, jota kutsutaan ns. näkyvän valon alueeksi. Tällä alueella ihminen aistii kolmea ns. pääväriä (sininen, vihreä ja punainen) sekä niiden sekoituksena syntyviä väriyhdistelmiä. Useimmat päiväaktiiviset linnut pystyvät kuitenkin havaitsemaan ihmisisilmälle näkyvän aallonpituusalueen lisäksi myös ns. lähiultraviolettia valoa (UV-A; elektromagneettinen säteily aallonpituusalueella 320-400 nm).

Lintujen kykyä havaita ultraviolettia valoa on tutkittu lähinnä käyttäyty-miskokein ja silmän fysiologiaa tutkimalla. Nykymenetelmin, lähinnä spektrofototai spektroradiometrisiä mittauksia käyttäen, tutkijat ovat havainneet, että esim. eräät lintujen ravintokohteista ja osa höyhenpuvun väreistä ovat erityisen näkyviä juuri ultraviolettialueella. Aikaisemmin on paljon tutkittu mm. höyhenpuvun väritystä ja tehty kokeita keinovaloympäristöissä, ja lintujen erilainen värinäkö on jätetty huomioimatta. Väitöskirjatyössäni tutkin näiden ihmisisilmälle näkymättömien signaalien merkitystä punakylkirastaan (*Turdus iliacus*) ja teeren (*Tetrao tetrix*) ravinnonvalintakäyttäytymisessä, ja kirjosiepon (*Ficedula hypoleuca*) sekä sinitiaisen (*Parus caeruleus*) puolisonvalinnassa.

Kahdessa ensimmäisessä osatyössä tutkin punakylkirastaan ja teeren väripreferenssejä keinovaloympäristössä, jossa vaihtelin ultraviolettivalon määrää. Tässä ravinnonvalintakokeessa linnuilla oli mahdollisuus valita kahden eri värisen marjan välillä, joiden makuero oli minimoitu. Kokeessa käytin tavallista mustikkaa (jonka vahakerros heijastaa ultraviolettia valoa) ja mustaa mustikkaa (joko luonnossa esiintyvä musta ns. tervamustikka tai tavallinen mustikka josta oli poistettu vahakerros). Linnut suosivat tavallista (ultraviolettia valoa heijastavaa) mustikkaa kun valoympäristöön oli lisätty ultraviolettia valoa, mutta söivät kumpaakin tyyppiä yhtä paljon jos ultravioletti valo oli poistettu valoympäristöstä. Kokeista voimme päätellä, että kumpikin laji pystyy aistimaan ultraviolettia valoa. Lisäksi kokeet indikoivat, että ultravioletti väri saattaa olla erittäin tehokas mainosväri juuri linnuille valoympäristöissä, joissa lyhytaaltoisen valon määrä on suhteellisen suuri.

Väitöskirjani lopuissa osatyöissä tutkin kirjosiepon ja sinitiaisen höyhenpuvuissa olevien ultraviolettisignaalien merkitystä. Sain selville, että kirjosieppokoiraan höyhenpuvussa olevan suhteellisen ultraviolettiheijastuksen määrä saattaa indikoida koiraan kuntoa. Koiraan höyhenpuvun suhteellinen ultraviolettiheijastus korreloi negatiivisesti koiraan kevätmuuton (saapumisajankohta pesimäalueille) kanssa: aikaisin tulleilla koirilla oli suhteellisesti enemmän ultraviolettiheijastusta höyhenpuvussa. Kevätmuuton ajoitus on tärkeää koiraan pesintämenestyksen kanssa: aikaisin tulleet koirat saavat parhaat reivit (joita naaraat suosivat), ja koiraan mahdollisuudet paritua myös toisen

naaraan kanssa ovat paremmat. Lisäksi sain selville, että höyhenpuvun ultraviolettiheijastus on voimakkaampi vanhoilla koirilla kuin nuorilla ja että naaraiden heijastus on matalampi kuin koiraiden. Neljännessä osatyössä tutkin, kuinka höyhenpuvun ultraviolettiheijastus vaikuttaa naaraan puolisonvalintaan. Kokeessa manipuloin koiraiden höyhenpuvun ultraviolettiheijastusta kemikaalein niin, että toisen koiraan ultraviolettiheijastusta alennettiin ja toisen hieman lisättiin. Kokeen mukaan naaraat suosivat koiraita, joiden ultraviolettiheijastus oli korkeampi. Ihmissilmälle linnut kuitenkin näyttivät samanvärisiltä. Viimeisessä osatyössä tutkin höyhenpuvun värin ja erilaisten pesintäparametrien (esim. pesyekoko, lentopoikasten määrä ja koko) välistä yhteyttä sekä kirjosiepolla että sinitiaisella. Tutkimuksen mukaan kuitenkin pelkkä väri on huono indikaattori yksilön pesimämenestyksestä.

Väitöskirjatyön osatutkimusten perusteella voin todeta, että lintujen erilainen värinäkö tulisi ehdottomasti huomioida kokeita suunniteltaessa ja niiden toteutuksessa, erityisesti kun tutkitaan lintujen väripreferenssejä tai lintujen höyhenpuvussa olevia värejä. Koska lintujen näkökyky poikkeaa ihmisen näkökyvystä, osa lintujen saamasta informaatiosta saattaa jäädä meiltä huomaamatta. Toisaalta voimme nyky menetelmin hyödyntää tätä informaatiota tutkiessamme lintujen käyttäytymiseen vaikuttavia tekijöitä.

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Original papers

I

**Ultraviolet reflection of berries attracts foraging birds. A laboratory study
with redwings (*Turdus iliacus*) and bilberries (*Vaccinium myrtillus*)**

by

Heli Siitari, Johanna Honkavaara and Jussi Viitala

Proceedings of the Royal Society: Biological Sciences 1999, 266: 2126-2129

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II

Behavioural evidence on ultraviolet vision in tetraonid species – a foraging experiment with the black grouse (*Tetrao tetrix*)

by

Heli Siitari, Matti Hovi and Jussi Viitala

Manuscript (submitted), 2001

<http://dx.doi.org/10.1034/j.1600-048X.2002.330212.x>

III

Individual colour variation and male quality in pied flycatchers (*Ficedula hypoleuca*) –the role of ultraviolet

by

Heli Siitari and Esa Huhta

Manuscript (submitted), 2001

<https://doi.org/10.1093/beheco/13.6.737>

IV

Ultraviolet reflection and female mate choice in the pied flycatcher (*Ficedula hypoleuca*)

by

Heli Siitari, Johanna Honkavaara, Esa Huhta and Jussi Viitala

Initially accepted (*Animal Behaviour*, 2001)

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V

Colour and reproductive success in pied flycatchers and in blue tits

by

Heli Siitari

Manuscript, 2001

COLOUR AND REPRODUCTIVE SUCCESS IN PIED FLYCATCHERS AND IN BLUE TITS

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Summary. Colourful plumage may function as an indicator of mate quality, and both females and males may gain direct or indirect benefits by choosing colourful mates. However, although novel methods allow the exact colour determination it is still unclear how colour itself could signal parental quality. In this field study, I examined how human-invisible colour might be related to parental quality in terms of reproductive success in pied flycatchers and in blue tits. As parameters of reproductive success I used timing of breeding, clutch size, number of fledged young and fledging mass. Birds are also sensitive to the near ultraviolet light. Therefore, when measuring plumage colour I took into account the whole waveband of light over which birds are sensitive (320-700 nm). I found that colour is not related to parental quality, or at least the effects are weak in erratic environmental conditions. Even if I cannot exclude the possible weak effects of colour on reproductive success in blue tits, colour as an estimate of individual quality may be of limited use. However, further large-scale field studies are needed before definite conclusions are possible.

Key words: colour, reproductive success, ultraviolet, pied flycatcher, blue tit

Introduction

Bright and conspicuous plumage colours and colour-based signalling are common among many bird species. For example, in addition to physiological functions of the plumage coloration (for review see Savalli 1995), plumage colour is important in species recognition. In intraspecies signalling plumage colour may indicate e.g. sex, age and social status (Andersson 1994). Moreover, the evolution of bright plumage colours of males in sexually dichromatic species has often been explained by female choice. In this case plumage colour may indicate phenotypic condition or genotypic quality of the mates (Andersson 1994). If the plumage coloration indicates male phenotypic condition, females, when choosing brightly coloured males may benefit in terms of direct benefits, e.g. better breeding site (Keyser & Hill 1999), increased feeding rate of incubating female (Hill 1991) and the young (e.g. Hill 1991, Palokangas *et al.* 1994, Keyser & Hill 2000). In addition to the possibility of direct benefits, number of studies have provided evidence that females may obtain indirect genetic benefits by choosing males with elaborate traits (e.g. Andersson 1986, Møller 1994, Petrie 1994, Hasselquist *et al.* 1996, Sheldon *et al.* 1997, Møller & Alatalo 1999). Colour may also function as such a trait possibly indicating the genetic quality of the mate, e.g. in terms of better survival of the

individual (e.g. Sheldon *et al.* 1999) or indicating parasite resistance (Hamilton & Zuk 1982). If the colour is an honest signal of mate quality and there is a positive correlation between bright coloration of parents and the offspring, females by choosing colourful males may obtain indirect benefits for their offspring.

According to the theory of condition-dependent signalling, only males in good condition are able to pay the costs of the signal (Zahavi 1975, Grafen 1990, Johnstone 1995). Both clutch size and timing of breeding are probably constrained by parental condition (Perrins 1970, Jones & Ward 1976). Especially female condition is an important determinant of clutch size. Females in poor condition may lay a small clutch because they would not take care of a large brood (Lundberg & Alatalo 1992). Handicapping pied flycatcher (*Ficedula hypoleuca*) females by removing some tail and wing feathers decreased the clutch size compared to control females (Slagsvold & Lifjeld 1988). Moreover, females seem to adjust the clutch size also due to their mating status: monogamous females laid, on average, larger clutches than simultaneously laying primary and secondary females (Alatalo & Lundberg 1990). Timing of breeding is related to territory quality: first breeding pairs occupy the best breeding sites (Verhulst & Tinbergen 1991, Lundberg & Alatalo 1992, Møller 1994). In pied flycatchers, males that arrive earlier to the breeding sites increase their possibilities to become polygynous. Thus, arrival time has direct effects on male fitness (Alatalo *et al.* 1984). It is also suggested that high-quality females could reach breeding condition earlier and could mate with preferred males. This would then show an increase in male's reproductive success, although this may be due to more fecund females. Despite of this, the association between male character and female quality (measured as a timing of breeding and/or fecundity) provides strong evidence of female choice in monogamous species, like great tits (*Parus major*) and blue tits (*Parus caeruleus*) (Norris 1990).

The aim of this study is to investigate how plumage colour is related to parental quality in terms of reproductive success. When determining colours, I took into account also the ultraviolet part of light spectrum. This is because, in addition to human visible waveband of light (400-700 nm) birds are sensitive to the near ultraviolet light (UV-A 320-400 nm) (see for review Bennett & Cuthill 1994, Cuthill *et al.* 2000). As a model species I used pied flycatchers and blue tits. In pied flycatchers, territory quality of the male has shown to be the most important cue in female mate choice (Alatalo *et al.* 1986). Males are dimorphic in colour in the breeding time, but the human-visible colour has not major effects on female mate choice, or at least the results are divergent (Alatalo *et al.* 1990, Saetre *et al.* 1994, Saetre *et al.* 1997). However, UV coloration of males might be related to male quality. This is because proportional UV reflectance of the dorsal side of males was negatively related to male arrival time to the breeding sites (Siitari & Huhta, submitted manuscript), and altering of UV levels of dorsal side affected female mate preferences (Siitari, Honkavaara, Huhta & Viitala, submitted manuscript). Contrary to pied flycatchers, blue tit females are assumed to prefer a certain male trait (bright crown coloration), at least in controlled laboratory experiments (Hunt *et al.* 1998, Hunt *et al.* 1999). If females

would choose male character rather than territory quality, the colour might be positively related to reproductive success of males. Similarly, variation in male reproductive success must be due to variation in female quality rather than variation in territory quality. Finally, males with the brightest colour must attract the high quality females independently of territory quality. Thus, it might be that the relationship between colour and reproductive success is stronger in blue tits than in pied flycatchers. As parameters of reproductive success I used timing of breeding, number of laid eggs (clutch size), fledging success (number of fledged young in a nest) and mean mass of the young (in the age of 13 d). The mass of the young in the age of 13 d well describes the fledging mass in many passerine species (Perrins 1965, Lundberg & Alatalo 1992, but see Merilä *et al.* (1999)), which potentially has large positive effects on adult fitness (Williams 1966), lifetime reproductive success (Gustafsson 1989) and probability of recruitment (Linden *et al.* 1992).

Methods

Description of the study species

a) Pied flycatcher (*Ficedula hypoleuca*)

Pied flycatcher is a small migratory bird wintering in West Africa and breeding in wide areas in western and northern Europe. In Finland, the first males arrive to the breeding sites in the beginning of May. First females arrive, on average, one week after the first males (Lundberg & Alatalo 1992) and they use territory quality of males as a main cue for their mate choice (Alatalo *et al.* 1986). Egg laying begins in late May or in the beginning of June, normally five days after the weather has turned favourable (Lundberg & Alatalo 1992). Pied flycatchers have only one brood per breeding season. Part of the males become polygynous when males tend to feed only the nestlings of the primary brood (Lundberg & Alatalo 1992). The species is sexually dimorphic in colour in the breeding time. However, the dorsal side coloration varies also between males; some males become black while some remain female-like brown. There is no evidence that human-visible colour, inside the age classes, would affect male reproductive success in the field. Furthermore, dorsal side colour is strongly heritable (Alatalo *et al.* 1994), and thus, potentially it is a poor indicator of male quality. However, in our previous study we show that the proportion of ultraviolet in dorsal side is related to male arrival time to the breeding sites and thus, might be related to male quality (Siitari & Huhta, submitted manuscript). In an aviary experiment in which the UV chroma was either experimentally reduced or remain normal, females preferred males with non-reduced UV chroma (Siitari, Honkavaara, Huhta & Viitala, submitted manuscript). Thus, when territory quality was controlled for, females preferred males with proportionally more UV reflectance in their plumage.

b) Blue tit (*Parus caeruleus*)

Blue tit is a mostly monogamous bird with biparental care. Egg laying begins in early May in our study area, and pairs normally raise one brood per season. Although both sexes look quite similar to the human eye, males differ from females in the coloration of crown especially in the near UV waveband (Andersson *et al.* 1998, Hunt *et al.* 1998). Females seem to choose their extra-pair partners among males with the highest over winter survival (Kempnaers *et al.* 1997), and Sheldon *et al.* (1999) recently found that UV chroma (a measure of saturation) of crown predicts male overwinter survival. Also assortative mating according to the crown coloration in the field has been found (Andersson *et al.* 1998). Moreover, females adjust the sex ratio of their broods according to the UV chroma (a measure of saturation) of the crown of their mates (Sheldon *et al.* 1999). This means that females mated to males with high UV chroma of crown produced proportionally more sons than females mated to males with experimentally reduced UV chroma. Thus, UV coloration of crown is suggested to function as a sexual ornament and to be related to male quality.

Estimation of reproductive parameters and colour determination

I studied the breeding of pied flycatchers and blue tits in Konnevesi region (Central Finland) in the breeding season 2000. The start of breeding was defined as a day when first egg was laid. The nest boxes were checked every second day to determine the date of clutch initiation, assuming that one egg per day was laid (Lundberg & Alatalo 1992). If necessary, the initiation date was calculated regressively. After initiation of egg laying the nest boxes were visited regularly to determine the final clutch size. Hatching was determined by daily visits after 12th day of incubation assuming that hatching occurs 13-16 days after the clutch is completed in both species. Parents were captured using nest box traps for the colour determination. When nestlings were 13 d old I determined the number of young and weighed them individually using a Pesola spring balance to the nearest 0.1g. Blue tit nests were again inspected after fledging date to check for any dead young, so that the number of fledged offspring could be correctly determined.

In the laboratory I measured the colour of plumage of parents using a spectroradiometer (EG & G Gamma Scientific GS 3100 with EG & G RS-22 UV xenon fibre optic light source) from 320 to 700 nm (including the near ultraviolet area; 320-400 nm). The spectra were recorded in steps of 5 nm and calculated in relation to 98% white reflectance standard (LabSphereTM). From pied flycatchers I measured the reflectance from dorsal side (one measurement from the crest and back, respectively, see papers III and IV in this thesis). From blue tits I measured the crown reflectance twice. I then calculated the proportion of UV in each spectrum (UV chroma, $R_{320-400 \text{ nm}} / R_{320-700 \text{ nm}}$, see also Andersson *et al.* 1998, Sheldon *et al.* 1999, papers III and IV in this thesis), and then calculated the average UV chroma of the two spectra. In addition to UV chroma, I took into account the human-visible coloration in pied flycatcher

males and in blue tits. As a measure of visible coloration in pied flycatcher I used male brownness (proportion of brown colour in male's dorsal side). Females got always the score of 100. In blue tits, I calculated the visible chroma including blue-violet part of human-visible spectrum in addition to near ultraviolet spectrum (320-420 nm/320-700 nm, see also Andersson *et al.* 1998). This is because the peak of the reflectance spectrum of crown is around 420 nm indicating the hue of spectrum, and thus, it is very difficult to make any predictions from the colour vision system of blue tits (Andersson *et al.* 1998). After the measurements the birds were released back to their nest sites.

Data analysis

Values calculated as proportions were arcsine-squareroot transformed for the analysis. When the assumptions of parametric tests were not met, non-parametric tests were performed. All statistical probability values are two-tailed, and statistics were carried out using SPSS 10.0 for Windows.

Results

Examples of the reflectance spectra of both species are represented in Fig. 1. Males had higher UV chroma values than females in both pied flycatchers and blue tits (Table 1). Furthermore, age did not affect colour (Table 1) or reproductive parameters (Table 2) used in this study. Thus, in the forthcoming analyses I have separated females and males, but pooled two age classes (yearlings and adults).

The effect of colour on reproductive parameters in pied flycatchers (both females and males) was weak and correlation coefficients close to zero (Table 3). The same tendency was found also in blue tits, although fledging success was slightly positively related to female coloration (Table 3). However, in both species, timing of breeding was slightly negatively related to timing of breeding in females and males (Table 3).

I also analysed the degree of assortative mating in the study populations. I found no relationship between female and male UV chroma in either pied flycatchers ($r_p = -0.078$, $N=20$, $P=0.742$) or blue tits ($r_p = 0.217$, $N=13$, $P=0.477$). This was the case also when the waveband from 320 to 420 was taken into account in blue tits ($r_p = -0.021$, $N=13$, $P=0.976$).

Discussion

I did not find any positive or negative correlations between colour and reproduction success parameters either in pied flycatchers or in blue tits. The results are consistent with the recent study by Smiseth *et al.* (2001). However, I found a slight negative relationship between the timing of breeding and UV chroma in both pied flycatchers and blue tits. The effect was observed in both females and males, respectively.

Results concerning colour and reproduction success pied flycatchers are also consistent with results of the previous work (Alatalo *et al.* 1984, Alatalo *et al.* 1994) although I extended the determination of colour to the near UV waveband of light. It seems that females choose rather territory quality than male characteristics in this species in natural situation. This is concluded because male characteristics (UV chroma and/or visible coloration) did not affect the reproductive success parameters that I used in this study. Only timing of breeding and UV chroma were slightly negatively related. This was also found in females, which means that both males and females arriving early to the breeding sites might have proportionally more ultraviolet in their plumage. The UV chroma of females was not related to any other reproductive success parameters.

Is colour then an honest signal of mate quality? The studies concerning the topic in birds are scarce. However, in European kestrels (*Falco tinnunculus*) gain direct fitness benefits by choosing brightly coloured males. This is because bright males spent more time hunting, and thus, produced more offspring (Palokangas *et al.* 1994). In a study on blue tits (Sheldon *et al.* 1999) males with the bright crown coloration survived better than males with duller crown coloration, indicating male viability. These males are also preferred in extra-pair matings in blue tits (Kempnaers *et al.* 1997). In some other vertebrates, for example in fish, colour is related to parental quality (e.g. Berglund *et al.* 1997, Candolin 1999). Many of the previous work on this topic have been carried out on the species with carotenoid-based plumage ornaments (e.g. Hill 1990, Sundberg & Larsson 1994, Linville & Breitwisch 1997). However, Keyser & Hill (2000) found a positive correlation also between male structural-based coloration and male feeding rate. Contrary to their work, Smiseth *et al.* (2001) did not find such a correlation in their study on bluethroats (*Luscinia s. svecica*). Thus, further investigation on the honesty of colour signals is needed, especially concerning the honesty of structural-based colour signals in birds.

To conclude, there is no strong evidence that colour would serve as a good indicator of parental quality. This is because I did not find any certain relationship between colour and reproductive success. However, I can not claim that colour does not indicate parental condition at all. Furthermore, the weather conditions were extremely harsh and erratic in the study year and 39% of pied flycatcher nests and 41% of blue tit nests failed. In this study, erratic weather conditions might have affected reproductive success in an unexpected way. Thus, it is better to think this study as a preliminary study. More detailed long-term studies are needed to find out if there is any relationship between colour and parental quality.

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TABLE 1 Colour differences between sexes in pied flycatchers and in blue tits. Sex and age effects are tested with two-factor ANOVA (except effect of age on male brownness in pied flycatchers). All interaction terms (sex*age) are non-significant ($p>0.26$).

	two-factor ANOVA							
	females		males		sex		age	
	mean \pm SD	N	mean \pm SD	N	F(df)	P	F(df)	P
pied flycatcher								
UV chroma ¹ of upper side	10.66 \pm 1.40	26	15.39 \pm 2.13	21	66.19(1,43)	<0.001	0.038(1,43)	0.846
brownness of upper side ²	100	26	40.71 \pm 23.78	21	258.39(1,43)	<0.001	0.639(1,43)	0.429
blue tit								
UV chroma ¹ of crown	22.48 \pm 3.52	17	26.42 \pm 4.03	13	7.06(1,26)	0.013	0.097(1,26)	0.758
UV/violet chroma of crown ³	28.80 \pm 4.60	17	33.41 \pm 5.60	13	57.68(1,26)	0.010	0.014(1,25)	0.905

1 = $C_{UV} = (R_{320-400}/R_{320-700})$; 2 = proportion of brown colour in male's upper side, scored by human eye; 3 = $C_{UV/VIOLET} = (R_{320-420}/R_{320-700})$.

TABLE 2 Mean values \pm SD (sample size) of reproductive success parameters and effect of age on them. One-way ANOVA used.

		yearling	adult	df	F	P
		mean \pm SD	mean \pm SD			
pied flycatcher female	timing ¹	21.44 \pm 10.09 (18)	17.38 \pm 9.36(8)	1,25	0.938	0.342
	clutch size	6.11 \pm 1.02(18)	6.62 \pm 0.74(8)	1,25	1.621	0.215
	fledging success	5.11 \pm 1.28(18)	5.43 \pm 1.40(8)	1,25	0.296	0.592
	mean fledging mass	14.40 \pm 0.75(18)	14.49 \pm 0.69(8)	1,25	0.056	0.815
male	timing ¹	21.79 \pm 9.88(14)	19.14 \pm 9.41(7)	1,20	0.344	0.564
	clutch size	6.42 \pm 1.02(14)	6.57 \pm 0.98(7)	1,20	0.095	0.762
	fledging success	5.57 \pm 1.28(14)	4.71 \pm 2.36(7)	1,20	1.187	0.289
	mean fledging mass	14.27 \pm 0.60(14)	12.45 \pm 5.56(7)	1,20	1.557	0.227
blue tit female	timing ¹	10.55 \pm 5.63(11)	10.17 \pm 5.78(6)	1,16	0.017	0.897
	clutch size	9.91 \pm 1.38(11)	9.17 \pm 2.70(6)	1,16	0.576	0.460
	fledging success	6.27 \pm 2.28(11)	5.17 \pm 4.12(6)	1,16	0.520	0.482
	mean fledging mass	9.52 \pm 1.74(11)	6.62 \pm 5.21(6)	1,16	2.970	0.105
male	timing ¹	9.86 \pm 5.87(7)	11.50 \pm 4.28(6)	1,12	0.321	0.582
	clutch size	9.71 \pm 1.50(7)	9.17 \pm 2.71(6)	1,12	0.212	0.654
	fledging success	6.86 \pm 2.79(7)	6.83 \pm 2.23(6)	1,12	0.000	0.987
	mean fledging mass	10.21 \pm 1.28(7)	7.82 \pm 4.22(6)	1,12	2.053	0.180

Note: ¹= start of egg laying, numbers present days in May

TABLE 3 Spearman's coefficients of correlation (sample size) between colour characteristics and different reproductive parameters. All correlation coefficients are statistically non-significant.

		UV chroma	visible colour
pied flycatcher female	timing ¹	-0.203(26)	
	clutch size	-0.160(26)	
	fledging success	-0.270(26)	
	mean fledging mass (g)	-0.122(26)	
male	timing ¹	-0.270(21)	+0.207(21)
	clutch size	-0.189(21)	+0.229(21)
	fledging success	-0.023(21)	-0.047(21)
	mean fledging mass (g)	+0.042(21)	-0.964(21)
blue tit female	timing ¹	-0.219(17)	+0.051(16)
	clutch size	+0.206(17)	-0.163(16)
	fledging success	+0.113(17)	+0.452(16)
	mean fledging mass (g)	-0.038(17)	+0.318(16)
male	timing ¹	-0.089(13)	+0.209(13)
	clutch size	-0.180(13)	-0.072(13)
	fledging success	+0.070(13)	+0.115(13)
	mean fledging mass (g)	-0.363(13)	-0.165(13)

¹ = start of egg laying, numbers present days in May

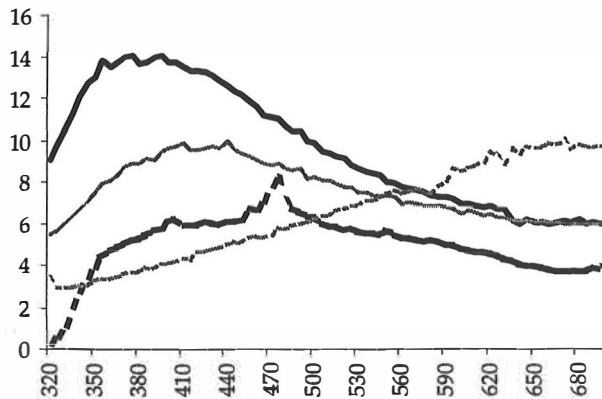


FIGURE 1 The two uppermost lines represent mean reflectance spectrum of five male (black solid line) and five female (grey solid line) blue tits. Black dotted line represent the mean reflectance spectrum of five black pied flycatcher males, and grey dotted line represent the mean reflectance spectrum of five brown pied flycatcher males. Pied flycatcher females are similar to the brown males.