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Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (Aves: *Luscinia s. svecica*): a field experiment

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The blue throat feathers of male bluethroats (*Luscinia s. svecica*) show a reflectance peak in the ultraviolet (UV) waveband (320–400 nm). The throat is actively displayed during courtship, suggesting a role for sexual selection on an ultraviolet signal. Indeed, a recent aviary experiment demonstrated that females discriminated against males with artificially reduced UV reflectance (Andersson & Amundsen 1997). Here, we report the results of a similar experimental manipulation applied on free-ranging males. UV-reduced (UVR) males had a lower success in attracting mates, as judged from a significantly later start of egg laying, compared with control (C) males. UVR males also spent significantly less time advertising for additional mates when their own mate was fertile, and they had a lower success in achieving extra-pair fertilizations. Furthermore, UVR males tended to guard their mates more closely and lose more paternity in their own brood than C males did. We conclude that the treatment affected both social and extra-pair mate choice. This is the first experimental evidence that UV signalling influences male mating success in free-ranging birds.

Keywords: UV vision; UV coloration; sexual selection; mate guarding; paternity; microsatellite markers

1. INTRODUCTION

The ability of many bird species to see ultraviolet light (UV, 320–400 nm), and the variable UV reflectance of ornamental plumages, suggest that avian sexual selection operates also in this (to humans invisible) waveband (Bennett & Cuthill 1994; Finger & Burkhardt 1994; Andersson 1996). Although the evidence is still scarce, aviary experiments have indicated effects of UV reflectance on female mate choice (Maier 1993; Bennett *et al*. 1996, 1997; Andersson & Amundsen 1997), and a recent study found UV sexual dimorphism and assortative mating in blue tits, *Parus caerulus* (Andersson *et al*. 1998). To our knowledge, however, there have been no experimental tests of the importance of UV signalling in sexual selection in free-ranging birds.

The bluethroat, *Luscinia s. svecica*, is a sexually highly dimorphic passerine, in which the male has a brilliant blue and chestnut throat patch. The blue parts of the patch reflect strongly in the UV (Andersson & Amundsen 1997). The male ornament is displayed both intra- and intersexually (Peiponen 1960). Sperm competition is strong, with males using mate guarding as a paternity assurance strategy (Krokene *et al*. 1996). Male bluethroats have an elaborate song, and a Finnish study reported a positive relation between song behaviour and pairing speed, suggesting an advertisement function of song in the species (Merilä & Sorjonen 1994). During the period of peak female fertility, males face a trade-off between mate guarding and singing (Johnsen *et al*. 1997).

In a cage experiment, Andersson & Amundsen (1997) coated the throat plumage of a group of males with a smear that absorbed UV but left the human-visible reflectance (400–700 nm) unaltered. The attractiveness of UV-reduced males to females was compared with that of control males receiving spectrally uniform (achromatic) brightness reduction, but retaining spectral shape (colour). They found that females associated significantly less with UV-reduced males. The authors concluded that females respond to UV in a mate choice situation, most likely using colour (hue) rather than brightness as a cue. To test whether the UV component of the colour signal affects mate choice in a natural population, we report here a field study in which we apply the same treatment to free-ranging bluethroat males.

Mate choice may be a two-step process: the choice of a social mate, and the choice of a genetic sire for the offspring (Møller 1992). These choices may be based on the same cues and coincide, but they may also differ. A previous experiment, in which bluethroat males with blackened throat patches gained lower pairing success than controls, indicated that the ornament colour was important in social mate choice (Johnsen & Lifjeld 1995). Blackened males guarded their mates more intensely and

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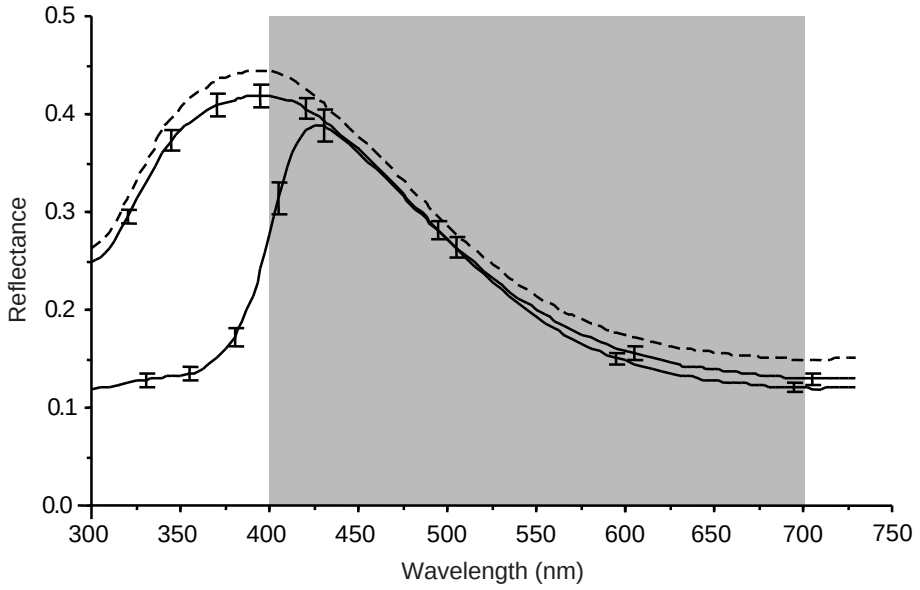

Figure 1. Average spectral reflectance (proportion of light reflected in relation to a white standard; see text) of the upper blue throat patch of bluethroat males in 1997, before (dashed line, $n=23$ males), and after (solid lines) either UV reduction (UVR, $n=11$ males, lower solid line) or control treatment (C, $n=12$ males, upper solid line). The two spectra from each male, pre- and post-treatment, were averaged from five and three scans, respectively, and multiplied by a factor setting the pre-treatment spectra to the average brightness (total reflectance 320–700 nm) of the population. To improve readability, standard error bars are spaced out and displaced in relation to each other. Shaded area denotes the 400–700 nm human visual range. For reflectance spectra from the 1996 treatment, see figure 1 in Andersson & Amundsen (1997).

sang less than control males when females were at peak fertility (Johnsen & Lifjeld 1995; Johnsen *et al*. 1998). Despite the increased mate-guarding effort, blackened males lost more paternity than controls, suggesting that females used the throat patch as a cue also in extra-pair mate choice (Johnsen *et al*. 1998). Similarly, a manipulation of the UV reflectance of the throat patch would be expected to influence both social and extra-pair mate choice. Following the results of the blackening experiment (Johnsen & Lifjeld 1995; Johnsen *et al*. 1998) and the aviary UV experiment (Andersson & Amundsen 1997), we made six predictions as to how a UV-deprived signal should affect male behaviour and mating success. Compared with a group of control males, we expected UV-reduced males to (i) acquire mates later, as indicated by onset of egg laying, (ii) guard their mates more closely, (iii) advertise (sing) less for additional mates, (iv) suffer a greater paternity loss, and (v) have lower extra-pair fertilization success. Finally, as a result of the latter two predictions, UV-reduced males should (vi) have a lower total fertilization success (within-pair plus extra-pair fertilizations).

2. MATERIALS AND METHODS

The experiment was carried out in Øvre Heimdalen (61°25′ N, 8°52′ E, 1100 m above sea level), Norway, during mid-May and early July in 1996 and 1997. Habitat and breeding biology of the dense bluethroat population in this area have been described in earlier studies (Johnsen & Lifjeld 1995; Krokene *et al*. 1996). Capture methods (mist nets and song playback), morphometric measurements, and blood sampling of adults and nestlings were also identical to previous experimental studies of this population (e.g. Johnsen & Lifjeld 1995).

(a) *Treatment*

Males were randomly assigned to either a UV reduction (UVR) or a control (C) treatment. As UVR treatment, we applied a fat coating to the blue parts and the chestnut spot of the throat plumage, using cotton swabs. The coating consisted of preen gland fat (CDC) mixed with UV-absorbing sun block chemicals, reducing reflectance below 400 nm but minimally affecting spectral shape in the human-visible range (figure 1). This technique has been employed successfully in an aviary experiment (Andersson & Amundsen 1997). Control males were treated slightly differently in the two years. In 1996, the control treatment consisted of the same preen gland fat, whereas the UV-absorbing substance was replaced by 2.5% Fe_2O_3 ('Oxide black'), which absorbs uniformly over the UV and human-visible spectrum. The black pigment was added to reduce signal brightness (radiance reaching the receiving eye under normal daylight conditions) of C males by the same amount as in the UVR treatment, in order to obtain primarily a colour difference (but a minimal brightness contrast) between the two treatments (see Andersson & Amundsen (1997) for details). In 1997, C males were coated with only the base substance (CDC), i.e. with no achromatic pigment added. We did this protocol change to avoid C males differing too much from unmanipulated males residing in adjacent areas (potential cuckolders). As a result, there was a contrast between the UVR and C treatments in 1997 in both colour and brightness (figure 1). Obviously, the 1997 design, and the two years pooled, only allow an effect of the UV signal component to be tested, whereas the relative importance of colour (hue and chroma) versus achromatic brightness cannot be inferred.

For 52% of the males (44 out of 84), reflectance from the upper throat plumage was measured (by S.A. and J.Ö.) before and after treatments (visualized for the 1997 treatment in figure 1). As described in more detail in Andersson & Amundsen (1997), reflected radiance in the 365–700 nm range was measured with a PS1000 spectrometer (Ocean Optics Inc., Dunedin, USA), a regulated tungsten–halogen light source, and in relation to Spectralon^{TM} white standard. The fibre-optic probe, with unidirectional illumination and recording, was held perpendicularly against a 5 mm wide measuring area in the centre of the chin plumage, removing the probe between each of 3–5 scans. Reflectance shape in the 300–365 nm range was extrapolated using the average from 20 museum specimens

(Göteborg Natural History Museum), and two treatment-coated study skins, respectively, measured in the full 300–700 nm range. There was a strong correlation between reflectance at 375 nm and 325 nm, and no evidence of increasing variation below 375 nm (see Andersson & Amundsen (1997) for further details). The extrapolation should therefore be a reliable estimate of the pre- and post-treatment reflectances.

As in the cage experiment, colour and brightness changes were invisible to the human eye. The effect on UV reflectance weakened over time, but a few recaptured UVR males in 1996 showed that more than 90% of the UV reduction remained 2–4 d after treatment (three males) and more than 50% after 12 d (one male). Because males were treated on average 12.5 d (range 7–20 d) before egg laying, and we were looking at effects in the pre-fertile and fertile periods, we are confident of a significant effect on UV reflectance during this time.

Most males (69 out of 84) were caught after territory establishment, four males (3 UVR, 1 C) established territories elsewhere in the study area, and 11 males (7 UVR, 4 C) disappeared after treatment. Using the criteria established by Johnsen *et al*. (1997), 64 out of 73 territorial males were judged to have been caught before pairing. Male territories were observed daily to record female visits, nest building and start of egg laying. Because of the cryptic behaviour of females and loose associations between pair mates, we were unable to determine the exact date of pair formation. We therefore used the date of first egg as a measure of pairing success, assuming that pairing and egg laying are connected in time. This assumption seems valid in migratory species in which breeding activities start shortly after female settlement (e.g. the pied flycatcher, *Ficedula hypoleuca* (Alatalo *et al*. 1984)), but less so in species with delayed breeding (e.g. the tree swallow, *Tachycineta bicolor* (Stutchbury & Robertson 1987)). Twelve nests were found after clutch completion and their first-egg dates were estimated by backdating (Johnsen & Lifjeld 1995). One UVR male apparently remained unmated, and to be able to include him in the analysis of laying dates, he was conservatively given a laying date of one day later than the latest first-egg date**.** There were no significant differences in capture date, standard body measures or age between UVR males and C males, nor between the females of the two groups (data not shown).

When nest building was almost completed, we started recording time budgets (duration 20 min) on pairs, scoring the distance between mates every other minute, and whether the male had sung during the preceding two-minute interval (see Johnsen & Lifjeld (1995) for a detailed observation protocol). All observations were done blindly (by A.J., J.Ö. and J.T.L.) with respect to treatment. We recorded time budgets on day -2 and/or -1 for 16 UVR and 27 C males. Estimates of mate-guarding intensity on these two days are typically correlated (Johnsen *et al*. 1997), and we used the mean of the two days when we had data from both. Observations were spread out over the day, with an unforeseen tendency for C males to be observed later during the day than UVR males (mean start of observations 1212 h and 1042 h, respectively, $Z=-1.86$, $n=47$ and 28, $p=0.063$). As a measure of mate-guarding intensity we calculated the proportion of time males were less than 1 m from their mates, whereas song rate was expressed as the proportion of two-minute periods with male song.

(b) *Analysis of parentage*

A set of six microsatellite markers (*FhU2*, *FhU3*, *HrU7*, *Phtr2*, *Pocc5* and *Mcyμ4*), isolated from five passerine species (pied flycatcher, *Ficedula hypoleuca* (Ellegren 1992; Primmer *et al*. 1996); barn swallow, *Hirundo rustica* (Primmer *et al*. 1995); willow warbler, *Phylloscopus trochilus* (Fridolfsson *et al*. 1997); crowned willow warbler, *P. occipitalis* (Bensch *et al*. 1996); and superb fairy wren, *Malurus cyaneus* (Double *et al*. 1997)) were used to determine parentage of 341 chicks from 65 broods. Using allele frequencies of 45–81 putatively unrelated individuals from the 1996 population and 63–108 individuals from 1997, the marker set gave exclusion probabilities (Jamieson 1994) of 0.995 and 0.996 for the two years, respectively. To save time and costs, the *FhU3* marker was only applied in cases where the other five markers did not produce a conclusive result. Exclusion probabilities for the remaining set of five markers were 0.986 and 0.989, respectively.

(c) *Statistical analyses*

Probability values are two-tailed unless otherwise stated. One-tailed tests were applied when we had a prediction of a directional difference (based on previous empirical work, see § 1). In the six variables used to test our predictions, there were no significant differences (all $p>0.19$) within treatment groups between the two study years. We therefore include analyses for both years combined. However, to avoid pseudoreplication, three individuals (two males, one female) that bred in both years were included only with the first year's data in the combined analyses.

3. RESULTS

(a) *Parentage*

For 231 of the 341 chicks, there were no mismatching alleles in any of the five loci. The average probability of false inclusion (Jeffreys *et al*. 1992) was 0.0095 ± 0.013 (range 1.6×10^{-5}–0.063) for these chicks and they were therefore considered genetically related to both attending parents. Of the remaining 110 chicks, seven had one and 103 had two or more mismatched loci. For 101 of the chicks with two or more mismatches, the father did not match with respect to at least one locus, whereas the female matched an allele in all six loci. These chicks thus resulted from extra-pair fertilizations. Two chicks showed mismatch with both parents at one or more loci, thus resulting from egg dumping. For four of the seven chicks with one (male) mismatch, neighbouring males matched the paternal genotype completely. The probability of false inclusion was 2–17 times lower for the neighbours than for the attending males (excluding the locus with the mismatch), and we consider these chicks to have been sired by the former. The remaining three chicks had no alternative sires within our sample and low average probabilities of false inclusion for the putative males after excluding the locus with the mismatch (0.002, 0.002 and 0.0002, respectively). The mismatches were therefore probably due to mutations (at three different loci).

In sum, 105 out of 341 chicks (31%) resulted from extra-pair fertilizations, two were the result of egg dumping (one in each year) and the rest were related to both putative parents. The extra-pair young were distributed in 38 of the 65 broods (58%). Split by year, the figures were 33 out of 99 chicks (33%) in 12 out of 18 broods (67%) in 1996, and 72 out of 242 chicks (30%) in 26 out of 47 broods (55%) in 1997.

A major advantage with microsatellite typing is that genetic sires can be searched for among all sampled males. We were able to assign paternity unequivocally (i.e. single males matching the paternal genotype completely) to 45 extra-pair chicks. Of these, 32 (71%) were sired by nearest neighbours and another 10 by males residing two or three territories away (i.e. 93% sired by males residing within three territories). Six additional chicks had between two and four potential sires. In all these cases, one of the possible sires was a male residing between one and three territories away (<350 m), whereas all other candidates resided more than 500 m away. It seems likely that these chicks were sired by the nearest male. The remaining 54 chicks (51%) must have been sired by unknown males from outside of the study area.

(b) *Treatment effects*

There was no significant difference between the two male groups in ability to retain the original territory (both years combined: UVR, 32/42; C, 37/42; Fisher's exact test, $p=0.25$), suggesting that the manipulation had little or no direct effect on male–male interactions.

If UV plays a role in female choice of social mate, one would expect UVR males to have lower success in attracting mates than C males, leading to a later pairing date for the former. Indeed, females of UVR males tended to start laying later than females of C males in both years, with significant differences in 1997 and in the combined data set (table 1).

Assuming that UV affects female choice of copulation partner, several predictions can be made concerning paternity and behaviour related to sperm competition (e.g. UVR males should guard more, sing less, have lower success in extra-pair copulations and lower paternity; see § 1). UVR males spent on average 12% more time closer than 1 m from their mates, but this difference was not statistically significant (table 1). C males had a significantly higher song rate than UVR males in 1996 and in the combined data set.

There was no significant difference between the two groups in paternity loss, although there were tendencies for a higher proportion of UVR males to have one or more extra-pair young in their nest (both years combined: Fisher's exact test, one-tailed $p=0.12$) and for UVR males to have more extra-pair young on average (table 1). However, a significantly higher proportion of the C males obtained extra-pair fertilizations in the combined data set. This test included all males that were territorial in the area at least up to the period when most females had started egg laying. Summing the number of legitimate young in their own nest and the number of young sired through extra-pair fertilizations, C males tended to have a higher total fertilization success than UVR males, but the difference was not statistically significant. Only males with DNA-analysed broods were included in this comparison.

In sum, all treatment effects, in each year and combined, went in the predicted direction of a negative impact on indicators of male sexual attractiveness and mating success, although many of them were not statistically significant.

4. DISCUSSION

Males that had the UV reflectance of their throat patch reduced (UVR males) started breeding later, sang less, and had a lower success in getting extra-pair young in other males' nests, compared with control males (C males). In addition, there were tendencies for a higher mate-guarding intensity, lower paternity and lower total fertilization success for UVR males.

This strongly suggests an effect of UV coloration on female preferences also in wild bluethroats, supporting the results of the cage experiment of Andersson & Amundsen (1997). The manipulation delayed acquisition of a social mate (assuming that laying date reflects pairing date) and lowered success in getting extra-pair fertilizations. Could these results be explained by male–male interactions rather than female choice? We find this unlikely for the following reasons. First, more than 94% of the males that settled in the area were treated after territory establishment, and there was no significant difference between the treatment groups in the proportion that disappeared. Owing to the random assignment of males to treatment, it is highly unlikely that the effect on timing of egg laying was a consequence of differences between the groups in territory quality determined by male–male competition. Second, because forced copulations do not seem to occur in this species (own observations), trait-related extra-pair fertilization success most likely reflects female preferences rather than male dominance. Third, Andersson & Amundsen (1997) showed in their cage experiment that females indeed had preferences for C males over UVR males, a result that was not affected by male–male competition. We conclude that males with reduced UV reflectance were less attractive to females in both social and extra-pair mate choice.

It must be stressed that the UV manipulation extended outside the natural variation in UV reflectance. We can therefore not exclude the possibility that females preferred normally looking males as opposed to males with UV-deprived throat coloration. In other words, we do not know whether natural variation in male UV reflectance (or any other component of throat colour, for that matter) is used as a mate-choice cue by female bluethroats in the wild. However, male UV coloration may be partly age-dependent in this population, as indicated by Andersson & Amundsen (1997), although this result did not seem to be upheld in our sample of males (S. Andersson, A. Johnsen, J. T. Lifield and J. Örnborg, unpublished data). Assuming that age reflects quality in some respect (e.g. breeding experience (Forslund & Pärt 1995)), this means that females may use the male UV ornamentation to choose males of higher quality (Andersson & Amundsen 1997). An interesting parallel is a previously overlooked sexual dichromatism and assortative mating based on a UV/violet plumage signal in blue tits (Andersson *et al*. 1998), a structural colour of similar type ('Tyndall blue') as in the bluethroats.

Because we did not control for brightness in 1997, we cannot determine whether females responded to colour (hue and chroma) or brightness in the UV. However, two lines of evidence suggest that colour *per se* contributed to the effects of the signal manipulation. First, the results were consistently similar in 1996 when we did equalize

Table 1. *Summary of between-group differences in six measured variables*

(UVR, males with experimentally reduced UV reflectance from the throat patch; C, control males. All *p*-values are one-tailed.)

	1996			1997			combined		
variable	UVR	C	test	UVR	C	test	UVR	C	test
laying date[a]	7.7±1.2 *n*=9	6.5±1.1 *n*=10	*t*=0.72 *p*=0.24[b]	8.0±0.5 *n*=20	6.6±0.5 *n*=23	*t*=1.86 *p*=0.035[b]	7.9±0.5 *n*=29	6.5±0.5 *n*=32	*t*=1.97 *p*=0.027[b]
mate guarding (prop. <1 m)	0.34±0.12 *n*=4	0.18±0.08 *n*=9	*Z*=1.19 *p*=0.12[c]	0.40±0.10 *n*=12	0.32±0.09 *n*=18	*Z*=0.57 *p*=0.28[c]	0.39±0.08 *n*=16	0.27±0.06 *n*=27	*Z*=1.22 *p*=0.11[c]
song (prop. of time singing)	0.17±0.13 *n*=4	0.58±0.09 *n*=9	*Z*=−2.39 *p*=0.008[3]	0.33±0.10 *n*=12	0.43±0.08 *n*=17	*Z*=0.73 *p*=0.23[3]	0.29±0.08 *n*=16	0.48±0.06 *n*=26	*Z*=−1.86 *p*=0.032[3]
paternity loss (prop. of EPO[f])	0.33±0.11 *n*=8	0.30±0.11 *n*=8	χ^2=0.13 *p*=0.36[d]	0.41±0.08 *n*=19	0.22±0.07 *n*=25	χ^2=2.25 *p*=0.067[d]	0.37±0.07 *n*=26	0.25±0.06 *n*=32	χ^2=1.74 *p*=0.093[d]
EPF success[g]	2 of 11 (18%)	4 of 11 (36%)	*p*=0.23[e]	5 of 24 (21%)	12 of 27 (44%)	*p*=0.068[e]	6 of 35 (18%)	15 of 37 (41%)	*p*=0.031[e]
total fertilization success	3.9±0.7 *n*=8	4.0±0.7 *n*=7	*t*=0.12 *p*=0.45[b]	3.7±0.6 *n*=19	4.7±0.5 *n*=23	*t*=1.41 *p*=0.084[b]	3.7±0.5 *n*=26	4.6±0.4 *n*=30	*t*=1.35 *p*=0.091[b]

[a] 1 =1 June. Median laying date was 7 June in both years.
[b] Student's *t*-test.
[c] Wilcoxon rank-sum test.
[d] Ordinal logistic regression testing the relationship between number of extra-pair offspring and treatment, controlling for brood size.
[e] Fisher's exact test.
[f] Extra-pair offspring.
[g] Extra-pair fertilization success, i.e. proportion of males that sired at least one chick in other males' nests.

signal brightness (i.e. the radiance reaching the receiving eye) between the two treatments. Second, the result of Andersson & Amundsen (1997) strongly suggested a response to colour independent of brightness in their outdoor aviary experiment. It therefore seems reasonable to conclude that this first evidence of intrasexual selection of UV signalling in a free-ranging bird population was based at least partly on colour perception.

Although there were several significant effects of the UV-reducing manipulation in this study, the magnitudes of these effects were rather weak compared with those in our earlier blackening experiment (Johnsen & Lifjeld 1995; Johnsen *et al*. 1998). The different responses may be explained by differences in the degree of manipulation and their effects on the sexual conflict over fertilizations (Johnsen *et al*. 1998). Another point is that the UV content of the male plumage ornament is only one of several cues on which females may base their mating decisions. Additional cues, including other chromatic or geometric (e.g. size) components of the throat patch as well as male display and song behaviour (Merilä & Sorjonen 1994), may also be important. Experiments on the bluethroat have indicated that there may be associations between several of these variables (e.g. Johnsen *et al*. 1998; this study).

In conclusion, this experiment has for the first time demonstrated an effect of UV signalling on both social and genetic mate choice in a wild bird population. As evidence for sexual selection outside the range of human vision, it has obvious implications for our understanding of avian colour variation and visual communication in general.

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REFERENCES

Alatalo, R. V., Lundberg, A. & Ståhlbrandt, K. 1984 Female mate choice in the pied flycatcher. *Behav. Ecol. Sociobiol*. **14**, 253–261.

Andersson, S. 1996 Bright ultraviolet coloration in Asian whistling-thrushes (*Myiophonus* spp.). *Proc. R. Soc. Lond.* B **263**, 843–848.

Andersson, S. & Amundsen, T. 1997 Ultraviolet colour vision and ornamentation in bluethroats. *Proc. R. Soc. Lond.* B **264**, 1587–1591.

Andersson, S., Örnborg, J. & Andersson, M. 1998 Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proc. R. Soc. Lond.* B **265**, 445–450.

Bennett, A. T. D. & Cuthill, I. C. 1994 Ultraviolet vision in birds: what is its function? *Vision Res.* **34**, 1471–1478.

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Maier, E. J. 1996 Ultraviolet vision and mate choice in zebra finches. *Nature* **380**, 433–435.

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Lunau, K. 1997 Ultraviolet plumage colors predict mate preferences in starlings. *Proc. Natn. Acad. Sci. USA* **94**, 8618–8621.

Bensch, S., Price, T. & Kohn, J. 1996 Isolation and characterization of microsatellite loci in a *Phylloscopus* warbler. *Molec. Ecol*. **5**, 150–151.

Double, M. C., Dawson, D., Burke, T. & Cockburn, A. 1997 Finding the fathers in the least faithful bird: a microsatellite-based genotyping system for the superb fairy-wren *Malurus cyaneus*. *Molec. Ecol*. **6**, 691–693.

Ellegren, H. 1992 Polymerase-chain-reaction (PCR) analysis of microsatellites—a new approach to studies of genetic relationships in birds. *Auk* **109**, 886–895.

Finger, E. & Burkhardt, D. 1994 Biological aspects of bird coloration and avian colour vision including ultraviolet range. *Vision Res.* **34**, 1509–1514.

Forslund, P. & Pärt, T. 1995 Age and reproduction in birds—hypotheses and tests. *Trends Ecol. Evol.* **10**, 374–378.

Fridolfsson, A.-K., Gyllensten, U. B. & Jacobsson, S. 1997 Microsatellite markers for paternity testing in the willow warbler *Phylloscopus trochilus*: high frequency of extra-pair young in an island population. *Hereditas* **126**, 127–132.

Jamieson, A. 1994 The effectiveness of using co-dominant polymorphic allelic series for (1) checking pedigrees and (2) distinguishing full-sib pair members. *Anim. Genet.* **25**, 37–44.

Jeffreys, A. J., Allen, M. J., Hagelberg, E. & Sonnberg, A. 1992 Identification of the skeletal remains of Josef Mengele by DNA analysis. *Forensic Sci. Intn* **56**, 65–76.

Johnsen, A. & Lifjeld, J. T. 1995 Unattractive males guard their mates more closely: an experiment with bluethroats (Aves, Turdidae: *Luscinia s. svecica*). *Ethology* **101**, 200–212.

Johnsen, A., Lifjeld, J. T. & Rohde, P. A. 1997 Coloured leg bands affect male mate-guarding behaviour in the bluethroat. *Anim. Behav.* **54**, 121–130.

Johnsen, A., Lifjeld, J. T. & Rohde, P. A. 1998 Sexual conflict over fertilizations: female bluethroats escape male paternity guards. *Behav. Ecol. Sociobiol.* (Submitted.)

Krokene, C., Anthonisen, K., Lifjeld, J. T. & Amundsen, T. 1996 Paternity and paternity assurance behaviour in the bluethroat, *Luscinia s. svecica*. *Anim. Behav.* **52**, 405–417.

Maier, E. J. 1993 To deal with the 'invisible'. On the biological significance of ultraviolet sensitivity in birds. *Naturwissenschaften* **80**, 476–478.

Merilä, J. & Sorjonen, J. 1994 Seasonal and diurnal patterns of singing and song-flight activity in bluethroats (*Luscinia svecica*). *Auk* **111**, 556–562.

Møller, A. P. 1992 Frequency of female copulations with multiple males and sexual selection. *Am. Nat.* **139**, 1089–1101.

Peiponen, V. A. 1960 Verhaltensstudien am Blaukehlchen (*Luscinia s. svecica*). *Ornis Fenn.* **37**, 69–83.

Primmer, C. R., Møller, A. P. & Ellegren, H. 1995 Resolving genetic relationships with microsatellite markers: a parentage testing system for the swallow *Hirundo rustica*. *Molec. Ecol.* **4**, 493–498.

Primmer, C. R., Møller, A. P. & Ellegren, H. 1996 New microsatellites from the pied flycatcher *Ficedula hypoleuca* and the swallow *Hirundo rustica* genomes. *Hereditas* **124**, 281–283.

Stutchbury, B. J. & Robertson, R. J. 1987 Do nest building and first egg dates reflect settlement patterns of females? *Condor* **89**, 587–593.