

Brief report

Bright colours and predation risk in passerines

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1. Introduction

The plumage colour of diurnal birds varies strongly from cryptic to bright and conspicuous. The sexual selection theory (e.g. Zahavi 1975, Andersson 1994) predicts a positive correlation between plumage brightness and predation risk, whereas the unprofitable prey hypothesis (Baker & Parker 1979, UPH hereafter) predicts a negative correlation. The UPH assumes that bright coloration would be an aposematic signal to potential predators that an individual or a species is difficult to catch or otherwise unprofitable, e.g. aggressive, unpalatable or poisonous. Thus, more cryptic individuals or species are predicted to suffer higher predation pressure than colourful ones. Evidence for the UPH has been provided by Baker and Hounscome (1983) in Britain, and Götmark (1992, 1993, 1995) and Götmark and Unger (1994) through exposing stuffed models of the sexually dichromatic and monochromatic passerine birds to sparrow hawks (*Accipiter nisus*) in the field.

To examine the relation between plumage brightness and predation risk, we compared predation rates of banded passerines by using banding return data in Finland and experimental data to find out whether conspicuous plumage exposes the bearer to higher or lower predation risk. In the prey choice experiment, we directly manipulated

brightness of colour patterns of great tits (*Parus major*) and presented great tits with dulled and naturally bright plumages in cages to Eurasian kestrels (*Falco tinnunculus*) in an aviary to study how plumage brightness of a prey affects attacks by falcons.

2. Methods

Banding return data on passerine birds were from the years 1960–1990. For the selected species ($N = 23$, 634 individuals), sufficient data were available for analysis, the individuals were killed by a predator and they have quite constant plumage brightness throughout the year. Five of the species were sexually dichromatic, with these we made a separate analysis for both sexes (Appendix). For each of these species we had access to information about age (ringmarked as nestlings), sex (male, female, unknown) and body length.

We have taken into consideration only birds with adult plumages. The selected species were ranked independently by 10 persons using a field guide on the basis of plumage brightness and conspicuousness; the range was from 1 to 20 (1 = most cryptic). Sexes of dichromatic species were ranked separately. The agreement on assessments was significantly consistent ($W = 0.63$, $\chi^2 = 163.2$,

df = 26, N = 10, P < 0.001, Kendal's concordance analysis). The mean value of ten ranks was used as a final value for brightness of each species and sex (Appendix). Since body size may also affect predation risk, we used as another morphological variable the mean body length of each species measured from the tip of the bill to the end of the tail (von Haartman et al. 1972).

Yearling birds, which were preyed on during their first year (before March of the second calendar year), were removed from the analyses because some passerines have fairly camouflaged juvenile plumages during their first autumn, and because we assumed that factors such as the inexperience of an individual could bias predation risk among young birds. We calculated the mean annual predation rates for each species and sex within species separately by using the formula:

$$l - s = \frac{N}{\sum x dx} \quad (1)$$

(Lack 1951). In the formula (1 - s) is the proportional mortality index, N is the total number of birds preyed on and $\sum x dx$ is the sum of preyed on (dx) individuals of each species during their x-th calendar year. The sum of each year is weighted by the number of years the bird survived.

We analysed the data following the taxonomy of Sibley et al. (1988). To control for the potential effects of common ancestry, we subtracted from the measured values of each species the mean values for its genus, leaving a set of residual values for species that were free of similarity between higher nodes (Stearns 1983). Since the original variables of predation rate and body length correlated strongly, we used in the final analysis predation rate adjusted body length, which was plotted against the residuals of the brightness variable.

In the aviary experiment, in each replicate we presented two great tits simultaneously in separate cages (67.5 dm³) to a captured kestrel. The aviary was lighted by ordinary mercury-vapour tubes and the background of both cages was kept constant by using a dark curtain. We used 26 falcons (14 males and 12 females, 12 adults and 14 yearlings) and 34 great tits in the study. Since hunger affects predatory behaviour, we did not feed the kestrels for 24 hours prior to an experiment as a way to increase their motivation to hunt.

Within each pair, a randomly chosen tit was painted on the bright parts of its plumage by using a black marker pen. The painted body parts were yellow sides of breast and belly, back, rump, white parts of ear coverts and neck and the outermost white tail feathers. Although the birds were not painted completely black, the original plumage colour was subsequently less conspicuous after removing the contrasts of the colour patterns. The behaviour of painted birds did not differ from unpainted birds in any observable way.

Kestrels observed tits from a 1.5-m-high perch that was placed 3 m in front of the cages, which were lying on the floor of the aviary. The kestrels were looking at the tits against the background formed by the dark curtain. Each pair of tits was presented to the kestrel for 30 minutes. To examine the effect of plumage colour on predation risk, we counted the number of attacks made by the kestrel on both tits. Possible genetic components of prey choice were examined by including yearling falcons, which were caught as fledglings and had no prior hunting experience. Finally, to avoid the problems of statistical independence, all birds were changed after each test and each bird was used only once in the experiment.

3. Results

For analysis of the banding return data, we included all 23 species of both sexes (both dichromatic and monochromatic). After controlling for the effect of body length and phylogenetic effects on predation rate and brightness, no correlation between brightness and predation risk was found (Fig. 1).

In the prey choice experiment we included in the analyses only the kestrels that attempted to attack (65%, N = 17). The response of falcons was not correlated with sex or age of the hawk (71% of males and 58% of females attacked, $\chi^2 = 0.49$, df = 1, P = 0.48; adults 67% and yearlings 64% attacked, $\chi^2 = 0.02$, df = 1, P = 0.90, Table 1). The great tits with natural bright plumages did not elicit higher rates of attack from the kestrels than did the experimentally dulled ones (Wilcoxon-test: T = 57.0, N = 16, P = 0.59, Table 1). Nor did the two groups differ in the duration of time to the first attack in relation to the target (natu-

rally coloured mean (min ± SD) 11.8 ± 9.9, N = 8; painted 5.1 ± 5.5, N = 9, Mann-Whitney U-test: U = 23.5, P = 0.25).

4. Discussion

After removing the effects of body length and phylogeny on predation risk and plumage brightness, there was no relation between brightness and predation risk. Thus, our data did not support the predictions of either the sexual selection theory or the UPH. In the prey choice experiment, it was possible to control for differences in the behaviour and the visibility of prey by using captured living birds. The falcons had a clear chance to choose between two different and simultaneously presented options of colourful and dulled prey, but they did not show preference for either of the prey targets.

The UPH states that predators may prefer prey items whose catchability they have learned or assessed to be easy on the basis of cryptic coloration. Another possibility is that choice of a particular prey type might be determined genetically. By using yearling falcons that had spent the whole of their life in captivity, we avoided possible problems of individual predators having previously formed search images for particular prey types. However, neither the yearling kestrels nor the adults showed any preference for a particular prey.

The sexual selection theory predicts that sexually selected traits are costly. An increased predation risk of an individual because of greater plumage brightness, as a result of sexual selection, would be expected to be such a cost. However, the sexual selection and the unprofitable prey theories do not necessarily predict that the existence of a correlation between predation risk and plumage brightness is the universal rule. For example, factors such as behavioural and sex role differences between males and females may also affect the predation risk of individuals. In species, which prefer sheltered habitats or have large body size, colourfulness might have evolved without a high risk of predation (Krebs 1979) or bright plumage colours might have evolved on the stage where a species is not exposed to a high predation risk (Andersson 1994).

We did not find any relation between plumage brightness and predation risk, which indicates

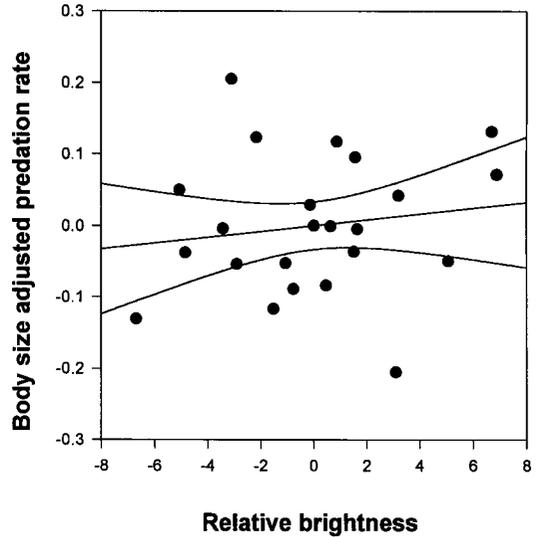


Fig. 1. The relationship between relative brightness and predation rate at genus ($\beta = 0.004$, $t = 0.77$, $df = 1$, 26 , $P = 0.45$, Fig. 1) level, controlling for the effect of body length and phylogenetically correlated variation in predation risk and plumage brightness following Sibley et al. (1988) taxonomy. Regression lines with 95% confidence limits presented.

that predation is a rather complex event and that it can be affected by many other factors not measured here. Our study may contain some methodological problems which might have hampered us in our efforts to discover a potential relation between brightness and predation in the analyses. First, it is unclear how good is the correspondence between predation rate measured using banding data and actual predation rate. Biases may arise in the recovery of carcasses of predation victims

Table 1. The total number of attacks made by the kestrels of different sex and age towards naturally coloured and dulled great tits. Between sexes $\chi^2 = 0.0$, $df = 1$, $P = 1.0$ and between ages $\chi^2 = 0.0$, $df = 1$, $P = 1.0$.

	Natural	Dulled
Male	9	13
Female	12	15
Adults	12	16
Yearlings	9	12
Total	21	28

which can be affected by prey size, habitat and plumage conspicuousness. Further, it is difficult to assess conspicuousness of animals quantitatively since all scores are not concordant, illustrating the problem of using subjective human judgement. The use of field guides as the judgement base for scoring visual conspicuousness, may not be the best method, since the pictures present close-quarter conspicuousness instead of long-distance conspicuousness, which might be more important in nature. Furthermore, some colour patterns may be less conspicuous close up than farther away.

The field guide ranking often represents conspicuousness which is independent of an effect of background contrast. In natural settings visual backgrounds consist of light and shadows, which could camouflage perhaps even very bright species efficiently (e.g. Endler & Lyles 1989). Moreover, quantifying conspicuousness in the field may be hampered by the fact that the visual background of individuals may vary strongly depending on the habitat where an animal lives. The definition of conspicuousness of a species in relation to a background is not unequivocal since ranking is done in regard to the prevailing circumstances (vegetation, light, weather, distance) and, therefore, absolute ranking could be impracticable. Another, more overwhelming, complexity is that the colour vision of birds differs from that of humans (Parrish et al. 1984, Viitala et al. 1995). Hence, colour patches that appear to be cryptic to humans may not necessarily be dull to avian predators.

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Selostus: Höyhenpuvun värikyyden merkitys predaatoriskissä

Seksuaalinen valintateoria ja epäsoipivasaalis teoria antavat päinvastaiset ennusteet höyhenpuvun värikyyden ja predaatoriskin välisestä riippuvuudesta. Seksuaalinen valintateoria ennustaa

värikyyden lisäävän kantajansa predaatoriskiä, koska pedot voivat helpommin havaita värikkäitä yksilöitä. Epäsoipivasaalis teoria puolestaan ennustaa, että pedot välttäisivät värikkäitä yksilöitä saalistuksessaan, koska teorian mukaan värikkyys toimisi aposemaattisena signaalina pedolle kantajansa epäsoipivuudesta saaliiksi. Epäsoipivuuden on otaksuttu ilmenevän saaliin kykynä paeta petoja tai saaliin pahan makuisuutena, mikä lisäisi pedon saaliinetsintä ja pyynti kustannuksia. Testasimme kummankin teorian ennusteita tutkimalla 23 suomalaisen varpuslintulajin predaatoriskiä rengastusaineiston valossa (yhteensä 634 yksilöä). Lisäksi teimme aviaariokokeen, jossa kaksi talitiaista, luonnollisen kirkas värinen ja kokeellisesti vähemmän kontrastikkaammaksi himmennetty yksilö, esitettiin tuulihaukalle. Rengastusaineistossa, huomioiden saaliin ruumiinkoon ja phylogeneettisen riippuvuuden, höyhenpuvun värikkyys ei korreloinut predaatoriskin kanssa. Aviaariokokeessa tuulihaukat eivät suosineet värikästä eivätkä himmennettyä talitiaista. Tuloksemme eivät siis tukeneet kumpaakaan esitettyä teoriaa.

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Appendix. Scores for predation rate, plumage brightness and body length (mm) of the passerine species used in the study. The brightness ranges from 1 (most cryptic) to 20 (most conspicuous).

	Predation rate	Colour score	Body length	N
Motacillidae				
<i>Motacilla alba</i>	0.62	14.8	279.0	12
Bombycillidae				
<i>Bombycilla garrulus</i>	0.71	12.4	273.0	17
Turdidae				
<i>Erithaeus rubecula</i>	0.61	10.8	209.0	62
<i>Turdus iliacus</i>	0.44	7.4	303.0	62
<i>Turdus pilaris</i>	0.54	7.4	378.0	57
<i>Turdus philomelos</i>	0.50	5.7	316.0	23
<i>Turdus merula</i>				
— male	0.36	6.3	380.0	12
— female	0.44	2.4	380.0	20
Muscicapidae				
<i>Ficedula hypoleuca</i>				
— male	0.57	15.9	189.0	15
— female	0.67	5.8	189.0	18
Paridae				
<i>Parus major</i>	0.62	16.6	217.0	407
<i>Parus caeruleus</i>	0.59	15.0	178.0	43
<i>Parus montanus</i>	0.55	8.5	194.0	29
Corvidae				
<i>Garrulus glandarius</i>	0.33	14.7	521.0	5
<i>Pica pica</i>	0.50	18.7	757.5	14
<i>Corvus corax</i>	0.43	8.6	902.5	19
<i>Corvus monedula</i>	0.37	6.2	492.5	5
<i>Corvus corone cornix</i>	0.40	8.3	695.5	22
Sturnidae				
<i>Sturnus vulgaris</i>	0.47	7.7	299.5	112
Passeridae				
<i>Passer domesticus</i>	0.68	4.3	225.0	49
Fringillidae				
<i>Fringilla coelebs</i>				
— male	0.59	11.8	228.0	35
— female	1.00	5.6	228.0	7
<i>Carduelis chloris</i>				
— male	0.57	11.1	217.5	24
— female	0.50	4.9	217.5	12
<i>Pyrrhula pyrrhula</i>				
— male	0.75	18.3	245.0	36
— female	0.77	9.7	245.0	35
<i>Acanthis flammea</i>	0.67	7.0	186.5	23
Emberizidae				
<i>Emberiza citrinella</i>	0.59	8.9	252.5	26
Total				634