Background matching and evolution of cryptic colours of selected passerines in deciduous woodlands

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Abstract

Most drab plumage colours are probably cryptic. Crypsis (camouflage) occurs when the colour of a significant part of the plumage is similar to the colour of a significant part of the background against which the prey bird may be detected by a potential predator. In this study we compare back colours of tits and associated species with colour backgrounds in their habitat during a four-month period in winter. We test the hypothesis that in some of the species back colour is similar to one of the background colours. In addition to colour backgrounds, microhabitats and tree species were also recorded. Great Tit *Parus major*, Nuthatch *Sitta europea* and Treecreeper *Certhia familiaris* showed distinct preferences for different colour backgrounds, reflecting their choice of microhabitats and tree species. The data suggest that in the Great Tit the olive-moss green back colour has evolved as crypsis for foraging close to the base of tree trunks, where most of the moss is found. The bluish-grey back colour of the Nuthatch is suggested to have evolved as crypsis against greyish beech trunks and branches. Similarly the brown back colour of the Treecreeper is suggested to have evolved as crypsis against pale brown- greyish brown bark surfaces. The possibility that the grey back colour of the Marsh Tit *Parus palustris* has evolved as crypsis against greyish branches is discussed. For the Blue Tit *Parus caeruleus* it is suggested that the green back colour has evolved as crypsis against leaves during summer; thus no background matching of the back occurs in winter. For the black back colour of the Longtailed Tit *Aegithalos caudatos* no background matching can be suggested. The study demonstrates that it is possible to quantify background colours for fouraging birds in the wild as seen by a human observer on the ground. It is proposed that these observations are also representative for a hunting Sparrowhawk *Accipiter nisus*, even though differences in observing height and possible differences in spectral visual range may present difficulties.

Key words:. Plumage colour, background colour, crypsis, Great Tit *Parus major*, Blue Tit *Parus caeruleus*, Marsh Tit *Parus palustris*, Nuthatch *Sitta europaea*, Treecreeper *Certhia familiaris*.

Introduction

Animal colours are thought to have diverse functions such as camouflage, intra- and interspecific signalling, thermal regulation plus protection against mechanical wear. Most often the colour pattern will be caused by multivariate selection pressures, each contributing to the combination of colours that maximises the overall fitness (reviewed by Endler, 1978 and Baker & Parker, 1979).

Excluding nest predation from Mustelids (*Martes* sp. and *Mustela* sp.), the Sparrowhawk *Accipiter nisus* is the predominant predator of small forest birds - amongst these tits and associated species - in northwestern lowland Europe (Tomialojc, 1984; Newton, 1986). It is presumed to have binocular colour vision (Endler, 1978; Bowmaker, 1986) and to depend on this when hunting (Newton, 1986). Therefore Sparrowhawk predation is assumed to have played an important role in the evolution of behavioural patterns, anti-predation tactics and camouflage colours of the prey species (Newton, 1986).

Colours serving anti-predatory purposes could be categorised as being either cryptic or aposematic. Since most European temperate forest passerines occur regularly in the diet of Sparrowhawks (Geer, 1982; Newton, 1986; Götmark, 1996), there is good reason to assume that the dominant colour patterns of its prey could have evolved as camouflage.

A number of studies by Götmark and coworkers (review Götmark, 1999) have attempted to elucidate the extent to which plumage colours and patterns are cryptic; f.i. by using mounted prey species placed in areas where high concentrations of predators occur during migration.

Crypsis occurs when the colour of a significant part of the plumage is similar to the colour of a significant part of the background against which the prey bird may be detected by a potential predator. For a quantitative assessment of crypsis measurements of background colour frequencies are therefore necessary.

Focus is here on the colour of the back (upper parts) of the prey species, assuming that the back generally is the most important part of the plumage in making a prey bird camouflaged. Background colours vary in most climates with season; species must be expected to vary with respect to in which season possible crypsis of the back occur.

The hypothesis to be tested in this study is, that the back colour in some of the species studied is similar to one of the background colours found in the habitat during winter.

The purpose of this study is to quantify the occurrence of common passerines in deciduous woodlands during winter on different colour backgrounds, microhabitats and foraging substrates and with these data test the hypothesis. Based on these data, the degree of colour resemblance between the dorsal side of the bird and the background, the simplest type of camouflage (Cott, 1940), is discussed.

Study sites and methods

Study sites

The fieldwork was conducted in four deciduous woods on the island of Zealand in Denmark. All were dominated by beech *Fagus sylvatica:* 1) Suserup Wood is an isolated unmanaged natural old-growth forest, containing all stages of succession (Møller, 1997). Apart from beech there are oak *Quercus robur,* ash *Fraxinus excelsior* and alder *Alnus glutinosa.* Structurally the 19 ha wood is approaching dynamic equilibrium (Christensen, 1993). 2) Næsbyholm Forest ("Enemærket") compromises 32 ha of straight-stemmed beech wood without understorey. The greater part of this is indigenous but intensively managed. Additionally it contains stands of ash and maple *Acer pseudoplatanus.* 3) The Strødam forest reserves ("Strødam II" plus contiguous forest) comprising 11 ha nog (natural old growth)-forest of which 7 ha is "primeval-like". The beech is mixed with oak, ash and forest elm *Ulnus glabra.* 4) Strøgårdsvang Wood comprising 24.5 ha of non-indigenous intensively managed forest like 2) interspersed by a few oaks. For further details on the localities, see Møller (1997).

Methods

Collection of data took place from 17 November 1997 to 19 March 1998 with a total of 72 field days evenly distributed over the period. The observations took place over 7 daylight hours, irrespective of the weather. The fieldwork took place in alternate weeks with 2 x 2 days at Suserup/Næsbyholm and 2 x 2 days at Strødam/Strøgårdsvang.

In order to ensure even coverage of the study sites, the observations took place along random transects, chosen by pulling random compass directions out from a bag. For every 100 metres' walk at about 2 km/h an observation stop was made. The surroundings were scanned until the first foraging bird was spotted and identified. Observations were commenced when the first "feeding peck" was seen. Data was recorded on a dictaphone for as long as possible (max. 2 minutes). For every individual, colour background, microhabitat and tree species were recorded. Non-foraging birds or individuals, that appeared to be affected by the presence of the observer, were not observed.

Colour backgrounds were divided into the following categories: *a)* dark olive green, *b)* moss green - olive green, *c)* light green (e.g. algae and lichens), *d)* grey (e.g. typical beech bark), *e)* pale brown (greyish brown - pale brown - brown) (e.g. typical oak bark, dry soil and dead wood without bark), *f)* reddish brown (e.g. dead beech leaves), *g)* warm brown (e.g.

wet dead wood in late decomposing stages), *h)* black (e.g. dead wood in late decomposing stages, bog soil), *i)* pale yellowish brown (e.g. dead grass), *j)* white (e.g. snow or birch bark), *k)* heterogeneous colour background (e. g. in situations where the bird, because it is situated on small branches, twigs or herbs and at a relatively great distance from the colour background, is perceived against a varied and poorly definable background). In those instances where it was seen against an uneven, but not strongly heterogeneous background, the background was categorised as belonging to the hue which dominated the colour mosaic. The observer has a normal colour vision.

Microhabitats were divided into: 1) forest floor, 2) dead wood, 3) trunks (> 30 cm), 4) large branches (8 - 30 cm), 5) branches (4 - 8 cm), 6) small branches (0.8 - 4 cm), 7) twigs (< 0.8 cm) and 8) herbs. Moreover the degree of decomposition was ranked on the following ordinal scale: 1) Fresh, the wood hard, bark intact, unchanged cross-section, 2) surface layer soft, bark loose or partly detached, unchanged cross-section, 3) wood soft several centimetres down, bark gone, 4) rotten throughout and full of holes, breaks easily, oval cross-section, 5) partly or nearly wholly decomposed (Møller, 1997). The trees were divided into beech, oak, ash, alder and other species.

If the bird changed substrate during the observation period, this was stated. If "feeding pecks" or "searching movements" (clear visual exploration of the substratum) were not seen as a minimum every 10 seconds, the observation period was discontinued. In order to define the available niche space (see below) foraging records were made on all species of foraging birds.

For birds foraging in 0-1 metre's height, it was noted if the bird was in dense cover. Equally it was noted if the bird was more than 2 metres from the nearest cover. If the bird was moving in the intermediate zone between trunk and forest floor (from 50 cm into the forest floor to 15 cm up the trunk - the "root zone"), this was recorded. The transect was continued when all birds at the observation post had been observed no more than once. If no birds were spotted at the observation post, it was abandoned after approx. 2 minutes. When the edge of the observation area was reached, a new random transect was pulled. The new direction had to be at least 40 degrees different from the direction of the previous transect.

Tapes were played back and converted into continuous time sequences on changing substrates which were subsequently converted to scanning observations (15 sec. intervals, n = 13484, each scanning obs. linked separately to the above-mentioned set of substrate categories and other measurements).

Data have been processed for the most common species only: Great Tit *Parus major,* Blue Tit *P. caeruleus,* Marsh Tit *P. palustris,* Longtailed Tit *Aegithalos caudatus,* Nuthatch *Sitta europea* and Treecreeper *Certhia familiaris.* The results from all four forests were pooled in order to get enough observations on quantitatively rare backgrounds. To ensure independent observations *only* the first observation ("1st obs.") of each bird was used for statistical tests. In order to test the significance of preferences weighted by the abundance of the different colour backgrounds, one-sample X^2 tests were performed. The expected number of observations of a given species against a given colour background have been calculated as: (Σ 1st obs. on the colour background *(all bird species)* / Σ 1st obs. on all

colour backgrounds (*all bird species*)) x Σ 1st obs. of a given bird species *(all colour backgrounds).* Preferences for microhabitats and tree species were calculated similarly.

Results

For all species it was significant that they were non-randomly distributed over the different colour backgrounds, microhabitats and tree species (p < 0.0001, one-sample X^2).

Table 1 shows that there is great variation between colour backgrounds with respect to which species are observed against them. Great Tit and Nuthatch show preference for olive- moss green and grey; the two species, respectively, have olive- moss green and grey backs. Nuthatch and Treecreeper show preference for pale brown; the latter species has a brown back. Great Tit shows preference for reddish brown. The three small tit species do not show preference for a particular colour but for a heterogenous background.

Table 1 - Frequencies (%) of observations on different colour backgrounds.

	O.	L.g.	G.	P.b.	R.b.	W.b.	B.	H.b.	I.n.	N
Great Tit *(P. major)*	7.3	1.8	21.5	4.5	10.6	0.5	0	36.3	15.3	786
level of significance	***		***		***					
Blue Tit *(P. caeruleus)*	2.1	0.4	6.9	1.2	3.7	0	0	81.5	4.5	729
level of significance								***		
Marsh Tit *(P. palustris)*	1.4	0.3	3.9	3.6	3.9	0.3	0	79.5	7.2	361
level of significance								***		
Longtailed Tit *(A. caudatus)*	0	0	0.6	0.6	0	0	0	98.7	0	159
level of significance								***		
Nuthatch *(S. europea)*	7.1	1.7	48.7	22.5	8	0	0	10.5	1.1	351
level of significance	**		***	***						
Treecreeper *(C. familiaris)*	5.4	2.9	15.8	70.9	0	0	0	4.1	1	316
level of significance				***						

O.= Olive-moss green; L.g. = Light green; G. = grey; P.b = Pale brown; R.b. = Reddish brown; W.b.= Warm brown; B. Black; H.b. = Heterogenous background; I.n. = In cover. Bonferroni corrected significance values: * = p < 0.006, ** = p < 0.001, *** = p < 0.0001.

Table 2 - Frequencies of 1st obs. (%) and preferences for different microhabitats and tree species.

	F.	D.	T.	L.b.	B.	S.b.	Tw.	H.	N	Be.	O.	A.	Al.	Ot.	N
Great Tit *(P. major)*	25.2	22.3	6.2	2.9	10.4	11	21.7	0.3	797	79	3.4	3.4	1.6	12.6	613
level of significance	***				***	***				***					
Blue Tit *(P. caeruleus)*	6.4	27.5	1.6	0	1.1	5	51.6	6.6	701	69.9	9	7.2	3	11.2	654
level of significance							***	***		(x)				***	
Marsh Tit *(P. palustris)*	7	13.5	1.1	0	4.2	7	66.8	0.3	355	52.9	11	20	11.9	4.6	329
level of significance							***					***	***		
Longtailed Tit *(A. caudatus)*	0	2.2	0.7	0	0	0	97.1	0	138	71.2	5.6	8.8	14.4	0	125
level of significance							***						***		
Nuthatch *(S. europea)*	8.8	35.9	18.4	16.1	14.1	4.2	2.5	0	354	72.1	16	7.1	1.9	2.5	323
level of significance		***	***	***	***					***	(x)				
Treecreeper *(C. familiaris)*	0	25.8	41.3	15.5	14.2	2.3		0	310	33.3	43	15	6.2	2.6	309
level of significance			***	***	***						***				

F. = forest floor; D. = dead wood; T. = trunks; L.b. = Large branches; B. = branches; S.b. = small branches; Tw. = twigs; H. = herbs; Be. = Beech *Fagus sylvatica; O.* = Oak *Quercus robur*; A. = Ash *Fraxinus excelsior; Al.* = Alder *Alnus glutinosaaw; Ot.* = Other tree species. Bonferroni corrected significance values (microhabitats: *x* =p < 0.006, *xx* = p < 0.001, *xxx* = p < 0.0001. Bonferroni corrected significance values (tree species: *x* = p < 0.01), *xx* = p < 0.002, *xxx* = p < 0.0002.

Table 2 similarly shows variation with respect to the microhabitats where the birds are observed. Thus the Great Tit is far more frequently observed on the forest floor than the Nuthatch.. Also with respect to tree species there is marked variation. Thus the Treecreeper and Marsh Tit have high preferences for oak and ash, respectively.

In some colour background categories the expected values were so small that the test could not be performed. These categories were therefore lumped within the following groups: green, grey, brown/black and yellowish/white. Observations that did not obtain sufficiently high values even within these categories (yellowish brown and white) were discarded.

88% of the Great Tits foraging more than 2 m from cover on the forest floor were found in the "root zone" (n = 65). At the study sites, this zone comprises an estimated 70 m^2/ha. Since approx. 90% (estimated) of the forest floor is without physical cover (more than 2 metres from physical cover)the root zone comprises approx. 0.8-1% of open forest floor. Had the birds been distributed "randomly" over the open forest floor, approx. 99% of the observations would have been outside the root zone. Only 8 out of 65 Great Tits were found outside the root zone, which is less than one eighth of what one would expect. However, in the root zone, the number of observations was 88 times the expected. Thus there is a distinct tendency for Great Tits to forage in the root zone when they are far from physical cover. Since the expected values for birds in the root zone are below one, this tendency cannot be tested with a chi-square test.

Sightings on olive moss green were mainly done on trunks, dead wood and forest floor (root zone). Most observations on grey backgrounds were made on beech. Pale brown was predominantly recorded on oak. Observations on reddish brown were almost entirely from the forest floor (litter) and the majority of 1st obs. on warm brown and black came from dead wood in late decomposing stages (Table 3).

Discussion

The underlying theme of this study has been to investigate the degree of background colour matching in selected forest birds during the winter season.. The results show that Great Tit, Nuthatch and Treecreeper have different specific background colour preferences. This, naturally, has to do with the fact, that they have different food preferences and thus microhabitat and tree species preferences. In an evolutionary perspective, it must be assumed that these substrate preferences have played an important part in selection for specific plumage colour combinations that match the background colours optimally.

Assuming that birds are actually conscious about how detectable they are on differing colour backgrounds, this may have reinforced the selection for particular colour patterns. The fact that male chaffinches cover their white wing patches when foraging on the ground (Götmark & Hohlfält, 1995), may indicate that birds are aware of how well they are camouflaged in a given situation.

Great Tit

Back colour is a rather dark rich yellowish-green. Great Tits were most often seen on heterogeneous backgrounds. The average foraging height was 7.0 ± 6.2 m. Sparrowhawks typically "scan" the forest from a height of 15-20 metres [from the upper third of the trees (Newton, 1986)]. This means that the heterogeneous background, against which it would be seen in winter, will be a mosaic of colours dominated by grey, pale brown and reddish brown shades (trunks, branches and forest floor). The dominant plumage colours are yellow, bluish-grey, moss green, black and white. Except for the bluish-grey feathers, no background matching of major importance is recognised. In mast years, however, the Great Tits forage primarily on beechnuts, which they find on the ground (Betts, 1955). The autumn of 1997 had the poorest production of mast in 7 years (The Danish Tree Improvement Station, pers. com.). In years with normal mast production, one would therefore expect more observations against the forest floor and correspondingly fewer against heterogeneous backgrounds.

Incidentally, approx. one third of the observations against heterogeneous colour backgrounds arises from smaller branches, where the birds are in reasonable physical cover

Table 3 - Frequency (%) of microhabitats contributing to the colour patches.

	F.	D.	T.	L.b.	B.	S.b.	Tw	H	Be.	O.	A.	Al.	Ot.
Olive-mossgreen	17.6	36.3	43.1	2	1	0	0	0	91.7	2.4	4.8	1.2	0
Light green	0	32.4	50	5.9	11.8	0	0	0	50	17.6	8.8	5.9	17.6
Grey	0.2	42	14.2	12	31	0	0	0	93.3	3	2	1.2	0.5
Pale brown	1	38.6	26.1	18.4	15.3	0	0	0	23.8	49.4	19.5	4	2.4
Reddish brown	100	0	0	0	0	0	0	0	0	0	0	0	0
Warm brown	16.7	83.3	0	0	0	0	0	0	ni	ni	ni	ni	ni
Black	31.6	68.4	0	0	0	0	0	0	ni	ni	ni	ni	ni
Heterogenous	0	16.3	0	0	0	10.7	70	3.4	62.5	6.2	16.1	6.3	9

F.: forest floor; D.: dead wood; T.: trunks; L.b.: Large Branches; B.: branches; S.b.: small branches; Tw.: twigs; H.: herbs; Be.: beech (*Fagus sylvatica*); O.: oak (*Quercus robor*); A. ash (*Fraxinus excelsior*); Al.: alder (*Alnus glutinosa*); Ot.: other tree species; ni: not indentified; ni = not identified (on wood these colours are most frequently found on heavily decayed lying trunks with no bark left).

behind the outermost twigs. Background matching in relation to heterogeneous backgrounds of the above-mentioned character can therefore be regarded as being of lesser importance.

The second most frequent colour background, against which the Great Tits foraged, was grey. As it has bluish-grey wings and tail it seems reasonable to assume, that these colours result in relatively good background matching, when seen from above. The birds had a significant preference for beech (table 2), the bark of which by and large is the only substratum which is grey (table 3). 86.4% of the observations on grey background were made on large branches and branches. When foraging here they are at least partly protected from Sparrowhawk attacks, because smaller branches and twigs in the outer reaches of the crown afford some physical cover. The greatest importance of bluish-grey as a camouflage colour must therefore be assumed to arise, when foraging on trunks in the lower strata. 55% of trunk observations on grey background were from the root zone. This will be discussed in the following.

Observations against reddish brown and olive moss green backgrounds comprised respectively 11% and 7.1% of all Great Tit observations. This is not surprising, since 25.2% of the observations were birds foraging on the ground. When seen on relatively open forest floor, which in beech forests is dominated by reddish brown shades, the bird is not particularly well camouflaged. 49.4% of the Great Tits that foraged away from physical cover on the ground were found in the root zone. In situations, when the bird is most exposed to attack (> 2 m from cover), 88-97% of the observations were in the root zone. When the birds are spotted here, they will typically be seen on a mosaic of reddish brown (litter), olive moss green (moss on roots and ground) and grey (typically beech bark). Because moss green matches the olive green back and grey matches wing and tail colours, the bird will be perceived as an olive green/ bluish-grey patch in a mosaic of almost exactly the same colours, resulting in an effective camouflage effect.

Investigations have shown, that in years of mast there is a greater quantity of food on open forest floor than in low cover (Nilsson 1979). This is presumably due to the fact that places with low cover are most often small clearings where old trees have collapsed. These patches are characterised by dense up-growth and ruins of dead wood. In these locations, there is obviously no overhanging crown to yield mast. In non-mast years, it is possible that the difference in food availability in the two patch types more or less evens out. Under these conditions it seems likely that major feeding advantages will not be achieved by leaving the safer patches. The more exposed a patch is, the more easily available or profitable the food must be for the bird to be tempted to take the chance (Todd, 1990; Nonacs, 1990). In years of mast, it is therefore likely that the trade-off between risk of predation and starvation will be skewed in such a way that foraging in exposed patches with a higher food yield will become more important than staying in safety. It is thus to be expected that there will be more Great Tits foraging on the open forest floor in mast years and thereby also in the root zone where the camouflage effect seems to be most pronounced.

The field work took place in relatively small woods. The incidence of exposed edges may be expected to lower the air moisture and thereby reduce the abundance of moisture demanding species of mosses (and lichens). If the field work

had taken place in an unfragmented "primeval forest", it could have been expected, that due to higher air humidity and longer forest continuity one would have had proportionally more observations against backgrounds of moss (and lichen). Moreover, many mosses and lichens are sensitive to air pollution, which further reduces their incidence (Odgaard et al., 1997). It may therefore be expected that the Great Tit has evolved the colour of its back in forest habitats, where moss green colours have been more dominant than they are today.

In summary, we put forward the hypothesis, that the olive green back of the Great Tit has evolved as camouflage adapted to feeding on moss-covered substrata. More specifically, the results of this study suggests that the dorsal colouration of the Great Tit has evolved as camouflage well suited for exposed foraging close to the base of tree trunks where the majority of moss is situated.

Blue Tit

Back colour is green with a grey cast. 81.5% of the Blue Tit observations were made against heterogeneous backgrounds. This preference is related to the fact that 63.3% of the observations were made on smaller branches, twigs or herbs. The data thus do not suggest that the back colour of the Blue Tit matches the background during winter. The green colour is considerably lighter and less yellowish than that of the Great Tit. It is a fairly good match of fresh beech leaves (unpublished measurements). We suggest that the back colour matches the colour of the canopy during summer, when the Blue Til predominantly fourages on twigs (Gibb, 1954).

Marsh Tit

Back colour is greyish-brown. By far the greater part of the observations were made against heterogeneous backgrounds (79.5%) which relates to 74.2% of the observations being made against small branches, twigs or herbs. Thus the data do not suggest that the back colour of the Marsh Tit matches the background during winter. However, Gibb (1954) found that during winter 31-45% of the feeding stations were on branches and only 11-22% on twigs. The back colour of the Marsh Tit resembles the colour of branches (grey to pale-brown; table 3) and we suggest that this colour match has evolved as camouflage. The discrepancy between Gibbs results and ours probably reflects that Gibb noted where the feeding bird was perched, while we noted the background of the perched bird seen in an approximately horizontal direction. A perched Sparrowhawk will mostly see the tit more or less from above and thus partially with a branch as background.

Longtailed Tit

Back colour is dull black. Practically all Longtailed Tits (98.7) were observed on heterogeneous backgrounds as 97.1% of the observations were on twigs. No birds were seen against a black background. The data thus do not suggest that the back colour of the Longtailed Tit matches the background during winter. The strongly contrasting black and white plumage in itself speaks against the colours of the upper parts having evolved to provide background matching.

Nuthatch

Back colour is uniform blue-grey. Nuthatches were most often seen foraging over grey (48.7%) and pale brown (22.5%) backgrounds. Since the χ^2 value for grey was by far the greatest, it may be assumed that the preference for this colour background is more pronounced and that grey is the colour most important to match in connection with camouflage. This fits well with a preference for beech (table 2). Since the bluish-grey back of the Nuthatch lies close to the average colour of the beech bark, the background matching is close to optimal when they forage on the background, against which they were most frequently seen - greyish beech trunks, large branches and branches.

In large parts of Europe the Nuthatch is both found in deciduous and mixed forests - frequently in oak forests (Harrap & Quinn, 1996). In fact, according to most literature, Oak (*Quercus* sp.) is the preferred foraging substrate of the Nuthatch (Rivera, 1985; Matthysen, 1998). Both studies were conducted in forests where oak was dominant and beech either rare or absent.

It is a well known phenomenon that predators tend to switch to the most abundant and easily accessible prey items (McNaughton & Wolf, 1979). The claimed universal preference for oak and other tree species with strongly fissured bark is most commonly explained by "more" arthropods on fissured bark compared with the smooth bark of beech. There seems to be no doubt that the diversity of arthropods is higher on oak (Nikolai, 1986). However, when discussing food preferences, it is important to consider the actual densities of the most abundant species. Comprehensive studies on bark arthropod fauna have demonstrated that the most common species on deciduous trees - *Carobodes labyrinthicus* (*Oribatei*), *Drapestica socialis* (*Araneae*), *Reuterella helvimacula* (*Psocoptera*) and *Tachypeza nubila* (*Brachycera* (*Diptera*)) constituted respectively 51.8%, 51.2%, 28.7% and 41.1% of the total number of individuals from the groups. All four dominant species were found in higher densities on beech compared with oak (3,6 : 1, 1.25 : 1, 4.3 : 1 and 3.8 : 1 respectively) (Nikolai, 1986). Investigations of Nuthatch stomach contents tend to show preferences for Coleoptera and Diptera (Nikolai, 1986; Cramp, 1993). It seems reasonable to suggest that small or soft skinned prey items such as microarthropods and psocids are strongly underestimated in analyses like this, simply because these prey items are degraded very quickly in the stomach. Comparative density studies of Coleoptera on beech versus oak in the wood diameters most relevant for the Nuthatch, do not seem to exist (Boy Overgård Nielsen, pers. com.). All told, these results indicate that the importance of beech bark as a substrate for prey items suitable for the Nuthatch might be underestimated.

Some possible explanations why Nuthatches are most often seen on oaks could conceivably be: 1) Unmanaged beech stands, old enough to support large enough quantities of its quantitatively most important foraging substrate: dead wood, are practically non-existing in the European forests of today. 2) Fragmentation and silvicultural practices have caused more arid microclimates on the bark surfaces, leading to lower abundances of algae, mosses and lichens (Søchting, 1997). The abundance of these substrates has furthermore been negatively influenced by air pollution and lack of forest continuity (Søchting, 1997). As the density of many arthropod groups is positively correlated with the abundance of epiphytic vegetation (Nikolai, 1986; Boy Overgård Nielsen, pers. com), it seems reasonable to suggest that the food availability on bark was higher in pristine forest habitats. As oak and other tree species with strongly fissured bark have very favourable micro climatic conditions in the grooves (Nikolai, 1986), it is possible that the arthropod fauna on oaks have been less vulnerable to changes of anthropogenic character. As a consequence it seems likely that beech may have had a greater importance as foraging substrate for the Nuthatch before human impact changed the conditions for the arthropod fauna. Even small arthropods are very easy to spot on the smooth beech bark (Boy Overgård Nielsen, pers. com.). When comparing the bills of Nuthatch and Treecreeper, the former does not seem to be as specialised for foraging on fissured bark as the latter. Consequently it could be imagined that Nuthatches in pristine forests might have had a greater chance of getting its fair share of arthropods on the beech bark where the prey is easily accessible. 3) Apart from foraging, the Nuthatch uses the deep cracks in oak bark for hoarding (Matthysen, 1998) and to wedge the nuts when crushing the shells open (pers. obs.). As the Nuthatch is rather poorly camouflaged on this substrate they are easily spotted here (pers. obs.). 4) The preferred tree species is largely determined by abundance and hence substrate/prey switching. Had the above-mentioned study taken place in other types of forest, it is conceivable that one would have obtained results that pointed more towards preferences for brownish coloured backgrounds.

A fair amount of observations were on pale brown surfaces. This is related to two circumstances. Firstly 16.4% of the observations were on oaks, the bark of which is mostly greyish brown - pale brown. Secondly 35.9% of the observations were on dead wood (table 2). The average grade of decomposition was 2.3 ± 0.5 (sd). At this stage, the bark starts falling off in flakes. 78.1% of the observations were on dead beech wood. The colour mosaic on this substrate comprises: *1)* grey on the outer surface of the bark, *2)* grey brown - pale brown from the exposed dead wood and *3)* chestnut on those parts where the sub-bark is exposed. Even though the bird under these circumstances will frequently be registered as foraging on a pale brown colour background, it will in actual fact be on the above-mentioned colour mosaic. This colour combination matches the colour patterns of the Nuthatch very well: 1) is quite similar to the colour of the upper wing and back, 2) lies relatively close to the grey brown - pale brown (buff) of the breast and belly and 3) is almost identical to the chestnut colour of the flanks and the vent.

All told, there is little doubt that the Nuthatch is well camouflaged on the substrates where it, according to this study, most frequently forages. To suggest that the Nuthatch originally evolved in beech (*Fagus* sp. and *Carpinus* sp.) dominated primeval forests is natural, but rather speculative.

Treecreeper

Back colour is warm brown boldly streaked white. The Treecreepers had a distinct preference for pale brown backgrounds (70.9%) caused mainly by the preference for oak.

Treecreepers normally seek food on old trees with heavily grooved bark (Harrap, 1996). The oak preference is undoubtedly connected to the fact that the bark of old oaks is much more heavily grooved than bark of old beeches for which it showed a negative preference (p < 0.0001). Moreover grey beech bark seems not to offer any optimal camouflage for this species (pers. obs.). The barks of the other commonly occurring tree species used by Treecreepers in the study area (e.g. ash and alder) are both more grooved and considerably more brownish than beech (table 3). Even though the Treecreepers had no definite preference for these tree species, no decidedly negative preference was found.

It therefore appears likely that the Treecreeper has evolved its colour patterns on its back as camouflage against grooved bark surfaces - surfaces that are most often perceived as pale brown - greyish brown. In large parts of its range the Treecreeper forages on conifers (Harrap 1996). Since the bark of most older conifers is greyish brown to brown and quite grooved (Mitchell, 1977), this choice of habitat fits in nicely with the hypothesis.

Sources of error

A Sparrowhawk sees colour resemblance much as a human observer does if two conditions are fulfilled: (1) The physical stimuli from the matching coloured objects must be similar; (2) The visual spectral ranges must be similar.(1) The physical stimulus is represented by the reflectance spectrum of the coloured surface in the relevant spectral region (Dyck, 1966). Grey and brown natural surfaces are represented by roughly straight curves in the human spectral range (400-700 nm) (Norris & Lowe, 1964). Grey and brownish plumage colours have reflectance spectra of similar shape (Dyck 1966, Finger & Burkhardt, 1994). Green plumage colours have reflectance spectra which match those of green vegetation (Dyck, l987 and unpublished measurements). We conclude, that condition (1) as a first approximation holds for the human visual range. As regards condition (2) then contrary to humans many birds have UV photoreceptors resulting in an ability to see UV light (350 - 400 nm in daylight spectral composition) (Finger & Burkhardt, 1994). Whether this also applies to Sparrowhawks is unknown. In a visual predator premium on high visual acuity undoubtedly exists. The wider the spectral range the more chromatic aberration, which reduces sharpness of the image, increases. We therefore find it unlikely, that UV is important in Sparrowhawk vision. But even if the UV-region is relevant, it will probably not change colour resemblance significantly. Both many natural surfaces and many plumages are characterized by low UV reflectance (Finger & Burkhardt, l994; Götmark & Hohlfält, l995; own unpublished measurements). Measurements of UV reflections from Chaffinch *Fringilla coelebs* and Pied Flycatcher *Ficedula hypoleuca* suggest that differences in human and avian perception of UV are no serious bias in field studies aimed at quantifying conspicuousness (Götmark & Hohlfält 1995 The colour resemblances between most green plumages and leaves do not extend into the UV region (unpublished spectral reflectance measurements). Crypsis obtained by 'arctic whiteness' in birds does not extend into UV (Potapov & Bennett, 2002). Differing patterns of metamerism (different perception of equivalent spectra) in

Sparrowhawk and human vision could theoretically cause some bias (Endler, 1993) but have never been investigated.

Most natural colours in the winter forest, e.g. trunks and litter, are relatively unsaturated. A characteristic for these colours is that they are perceived very differently in changing "ambient lights" (Endler, 1993) and degrees of moisture (pers. obs.). Obviously this will give a considerable bias to the judgement of especially grey - greyish brown - pale brown. Clean grey - bluish grey as seen on beech trunks rarely causes problems, but grey - brown as on dry and strongly illuminated oak trunks can be quite difficult to categorise. In these situations the observations were most often put into the category pale brown because it was percieved as distinctly more brownish than "beech grey". In moist weather the same pale brown surfaces will be perceived much more brownish (pers. obs.).

It would have been desirable to supplement the background colours used in this study with colourimetric measurements. Circumstances prevented this. We feel, however, that the written descriptions of the colours, in combination with the substrates with which they are associated, will make it possible in future studies to use the same colours if appropriate.

The observations were made by a human observer situated on the ground, while the hunting Sparrowhawk observes from a considerable height. If the distance between a prey bird and its background is small compared to the extent of the background colourpatch this difference is probably of little importance However, where the extent of the background colourpatch is small (e.g. the width of a branch), angle of observation is important (see discussion of Marsh Tit).

The fact that only the first observation of each bird was used might be thought to introduce a bias in that the individual showing poorest background matching is likely to be detected first. However, using all instead of only first observations resulted in percentages very similar to those presented here. First detection of the birds to a large extent was by hearing them.

The hypothesis

The hypothesis that the back (upper parts) colour in some of the species studied is similar to one of the background colours found in the habitat during winter is supported, since three of the species studied: Great Tit, Nuthatch and Treecreeper show this type of background matching. A fourth species: Marsh Tit likely also shows background matching, while two species: Blue and Longtailed Tit do not.

The present study therefore demonstrates that (1) it is possible to quantify background colours for fouraging birds in the wild, and (2) it is possible to obtain evidence suggesting camouflage function of dorsal plumage colours.

Experimental evidence with live birds supporting camouflage function has been presented by Götmark & Olsson (1997), who dyed underparts and head of Great Tit fledglings red and thereby increased predation rate by Sparrowhawks.

In a similar study (Dyck, unpublished) I experimentally changed the back colours of adult Great Tits to yellow or black. Sample size is small, but the data suggest that this changes predation rate (increase for black- and decrease for yellow-backed birds), measured as disappearance rate.

Avoiding predators by camouflage implies that the prey birds stay immobile (Götmark, 1999). Klump & Curio (1983) provided experimental evidence that tits freeze in response to a moving hawk model

Other strategies for camouflage colours than the one presented here are possible. Instead of resembling a particular background, the dorsal colour may resemble an average of the background colours present in the habitat. Thia may apply in particular to prey birds that attempt to avoid predators by moving into cover [comp. Götmark (1999)].

During early summer the tits and other small forest birds are at great risk from predation (Geer, 1978, 1982; McCleery & Perrins, 1991). When investigating the camouflage effects in plumage of forest birds, it is therefore obviously not enough to look only at background matching in the winter. During summer the Parus species change to feed among the leaves (Gibb 1954), where the greenish back colours of the Great and the Blue Tit provide camouflage. The green colour of the Great Tit is, however, closer to the colour of moss than to that of leaves (unpublished measurements). This fact together with the absence of background matching in the Marsh Tit in summer indicates that the back colours of the three tit species are primarily adapted to winter conditions.In order to get a comprehensive picture of which colour patterns could have evolved as camouflage designed for different substrates and colour backgrounds, it would be interesting to make a corresponding study of background matching during the breeding period. This would obviously involve practical limitations since the birds are very difficult to observe after the foliation.

Background matching is very hard to quantify for wild birds in natural foraging situations - partly because of the subjective judgement of colours and partly because of the often strongly heterogeneous backgrounds. The fact that the quantitative data for some species does not reveal any background matching of importance does not necessarily imply that their colours cannot have evolved as camouflage against avian predators. For several of the birds not showing any cryptic effect of plumage it could be argued theoretically that dominant parts of their colour patterns could be suspected to have adaptive advantages as camouflage (Bursell, unpubl. ms).

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