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Carotenoid-based plumage coloration reflects hemoparasite infection and local survival in breeding great tits

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Abstract Carotenoid-based sexual coloration has been hypothesised to be prevalent across many vertebrate taxa because it reliably reflects individual phenotypic quality in terms of foraging efficiency or health status due to the trade-off between signal colour and use of carotenoids for immune function and detoxification. We investigated the ventral, yellow coloration of breeding adult great tits (*Parus major* L.) in relation to sex, age, breeding habitat, local survival and infection status with respect to *Haemoproteus* blood parasites. The extent of plumage coloration (estimated as hue and lutein absorbance) was generally higher in rural than in urban birds. Males had higher values of hue than females. In both male and female yearlings, the plumage of unparasitised individuals had a greater hue of yellow than parasitised ones, while older males revealed the opposite pattern. The survival of infected yearlings was worse than that of uninfected yearlings, while the opposite was true for old breeders. Survivors had generally higher values of hue than non-survivors. These results are consistent with predictions of functional hypotheses, suggesting that carotenoid-based plumage coloration serves as a signal reflecting individual quality in terms of health status and local survival.

Keywords Carotenoids · *Haemoproteus* · Local survival · *Parus major* · Plumage colour

Introduction

Sexual differences in coloration comprised a major component of Charles Darwin's ideas on sexual selection (Darwin 1871). Such sex differences were assumed to impose costs, for example caused by predation, and thus had to be maintained in males due to their advantages in terms of mating success. A number of different categories of models of sexual selection have subsequently emerged and these can broadly be categorised according to the functional or arbitrary component of signals (Andersson 1994). Functional hypotheses suggest that the extent of coloration reflects aspects of the phenotypic or genetic quality of a signaller (Zahavi 1975; Hamilton and Zuk 1982). In contrast, arbitrary models of sexual selection are based on the assumption that signals become exaggerated for random reasons (Fisher 1930), or due to pre-existing biases in female preferences (West-Eberhard 1983).

Secondary sexual coloration can be categorised as structural or pigment based. The latter category comprises colours based on carotenoids, but also melanin- and porphyrin-based coloration. Carotenoid-based colours are very common among vertebrates (Fox 1976, 1979; Goodwin 1984), and particularly sexual dichromatism in birds often has a component of carotenoids (e.g. Gray 1996). Many studies have shown from observations or demonstrated experimentally that females prefer males with brighter carotenoid-dependent colours (e.g. Endler 1983; Burley and Coppersmith 1987; Hill 1990, 1991, 1994; Milinski and Bakker 1990; Zuk et al. 1990). Bacteria, plants, fungi and algae produce carotenoids that only can be obtained by animals indirectly through the food chain (e.g. Fox 1976, 1979; Goodwin 1984; Hudon and Brush 1990). The concentration of carotenoids in plasma or muscle tissue is generally positively correlated with the intensity of coloration of signals (Bletner et al. 1966; Goodwin 1984; Hudon and Brush 1990; Hill et al. 1994; Saino et al. 1999). Carotenoids are limiting since addition of carotenoids to the diet greatly enhances the brightness of coloration (e.g. Hill 1992, 1993 for data

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from captivity; Grether et al. 1999; Saino et al. 2000 for data from the field; see Møller et al. 2000 for a review). Pale carotenoid-based coloration is often associated with parasitism (Zuk et al. 1990; Houde and Torio 1992; Folstad et al. 1994; Skarstein and Folstad 1996; Thompson et al. 1997; see Møller et al. 2000 for a review) and low health status (Dufva and Allander 1995; Skarstein and Folstad 1996; Saino et al. 1999; see Møller et al. 2000 for a review). Relatively moderate experimental infections with *Coccidia* have been shown to reduce the body content of carotenoids by up to 80% (Bletner et al. 1966; Yvore and Mainguy 1972; Ruff et al. 1974).

The great tit is a common passerine breeding throughout deciduous forests of most of the Palearctic region (Gosler 1993). The social mating system is monogamy (Gosler 1993), with frequent extra-pair copulations as demonstrated by variable, but relatively high levels of extra-pair paternity (Gullberg et al. 1992; Lubjuhn et al. 1993; Blakey 1994; Verboven and Mateman 1997; Krokene et al. 1998; Strohbach et al. 1998). Males and females are generally similar in phenotype with the exception of the black breast stripe, which is larger in males than in females, and the yellow, ventral coloration. The black breast stripe is apparently not associated with sexual selection as determined by extra-pair paternity (Krokene et al. 1998; Strohbach et al. 1998). The biochemical basis for the yellow plumage colour is lutein and zeaxanthin (Stradi 1998). Previous studies have demonstrated that great tits obtain lutein and zeaxanthin directly from their food and deposit this in their plumage during moulting apparently without any conversion of the biochemicals (Partali et al. 1987). However, since zeaxanthin can be converted into astaxanthin by birds (Stradi 1998), and since the distribution of carotenoids differ dramatically among tissues, we also have to consider the possibility that metabolites of the two main carotenoids in the plumage of great tits may play a functional role in the physiology of great tits. The yellow ventral colour differs between sexes with males being more yellow than females (as measured using standard colour charts), age classes with adults being more yellow than nestlings, and habitats with great tits from deciduous habitats being more yellow than individuals from coniferous habitats (Slagsvold and Lifjeld 1985). A study of the relationship between coloration according to standard colour charts (which may have resulted in biased results (Endler 1990)) and blood parasite infection showed no significant correlations between colour and parasitism for three genera of Haematozoan parasites (Dufva and Allander 1995).

The main aims of the present study were to: (1) assess the difference in coloration between sexes, age classes and habitats, using more precise measures of feather colour that quantify the different components of coloration; (2) assess the relationship between haematozoan-infection status and plumage coloration in order to test whether colour predicts current health status after controlling for differences between sex- and age-classes of birds breeding in different habitats; and (3) test if plumage coloration reflects individual quality by examining local survival rates of great tits in relation to plumage colour and hemoparasite infection status.

Materials and methods

The study was carried out during 1998 and 1999 in two neighbouring (urban and rural) great tit populations breeding in nest boxes in and around Tartu (58°22′N, 26°43′E), south-east Estonia (described by Hõrak et al. 1995). The distance between the two study areas was 8 km. Adult great tits were captured on their nests when nestlings were 8 days old. Birds were sexed and classified as yearlings or older (≥2 years) according to plumage characteristics as described by Svensson (1992).

To identify blood parasites, a drop of blood was collected from the tarsal or brachial vein, smeared on two individually marked microscope slides, air dried, fixed in absolute methanol, and stained with azure-eosin. Slides were examined for blood parasites and leukocytes as described in Ots and Hõrak (1996) and Ots et al. (1998). Because *Haemoproteus* sp. was the only common blood parasite, with a prevalence of ca. 50% (Hõrak et al. 1998), we confined our examination of the prevalence of parasitemia to this genus.

Lutein and zeaxanthin are the major carotenoid components of ventral plumage colour in great tits (Stradi 1998). Colours cannot be measured objectively with the human eye (e.g. Endler 1990), and we used a highly sensitive photospectrometer that measures the major components of colour in the range of wavelengths between 300 and 800 nm. Analysis of plumage colour was performed on two feathers, plucked from a standard position on the breast: the midpoint between the upper part of the sternum and the edge of the wing. Subsequent to plucking, feathers were placed in a plastic bag and stored in darkness until measurements were made. Colour was measured in an area of the visible surface of the feather of approximately 1 mm^2 using a portable spectroradiometer (Ocean Optics Europe). Two feathers from each bird were placed one on top of the other and the mean of five or six measurements for each set of two feathers was averaged to obtain the individual values. Light from a halogen light source (DH 2000) was transferred to the feather through a quartz optic fibre (Ocean Optics), reaching the feather at 90°. The sampling optic was placed at 45° to the surface of the sample and connected to a spectrometer (S2000) by a second quartz fibre optic cable. Data from the spectrometer were converted into digital information by a DAQ Card 700 and passed into a computer with appropriate software (Spectrawin 3.1), which automatically transformed the spectra into values of absorbance, hue and saturation. The measurements were relative and referred to a standard white reference tile (WS-2) and to the dark. Each pair of feathers provided a measure of transmittance for each 1-nm interval in the range of 300–800 nm. Since lutein absorbance peaks at 450 nm (Stradi et al. 1995), absorbance due to this carotenoid was calculated from mean transmittance in the interval 445–455 nm, as $-\log_{10}$(transmittance value), and used for subsequent analyses. Additionally, we used values of hue obtained during the same measurement process. Both these variables reflected independent aspects of plumage coloration, as their correlation was very weak (r=0.06, n=421, P=0.23). Repeatability (Lessells and Boag 1987) of hue measurements was 0.56 in 1998 and 0.82 in 1999, and repeatability for lutein absorbance was 0.60 in 1998 and 0.77 in 1999 (all P <0.0001; 208 individuals and 1140 measurements in 1998; 231 individuals and 1276 measurements in 1999).

Relationships between colour and hemoparasite prevalence were examined in ANOVAs using colour parameters as dependent variables. To control for confounding factors such as sex, age, year and study area, all models were checked for the significance of these terms (and their interactions with parasitemia). To avoid pseudo-replication, a test sample was formed for analysing the pooled data. It included the birds captured only once and a randomly picked observation of individuals that were captured in both study years, so that none of the individuals was entered more than once in the analysis. Analyses were performed with the SAS GLM procedure (SAS Institute 1985), using type III sums of squares, enabling us to account for all effects of independent variables simultaneously. Correspondence of residuals to a normal distribution was checked with the SAS univariate procedure (Shapiro-Wilk's *W*-test); in no case was the assumption of normality violated. All significance levels refer to two-tailed tests. Subscripts used in connection with *F*- and *t*-tests refer to *df*. Values are means (SD).

Results

Hue

Male great tits had significantly higher hue values of breast plumage than females [on average a 6.4% difference; males, 68.1 (5.8), *n*=164; females, 64.0 (4.7), *n*=168], and rural birds had higher hue values than urban birds [on average a 4.2% difference; rural, 67.7 (4.8), *n*=124; urban, 65.0 (5.8), *n*=208; see Table 1 for significance levels]. The relationship between plumage hue and age differed between females and males (Table 1). Old females had lower values of hue than yearlings, while the difference was in an opposite direction for males (Fig. 1). In 1998, the average value of hue was higher [67.8 (6.4), *n*=151] than in 1999 [64.6 (4.4), *n*=181].

Table 1 Factors affecting hue of breast plumage colour in breeding great tits; R^2=0.34

Effect	F_{df}	P
Haemoproteus	$0.0_{1,331}$	0.96
Sex	$53.6_{1,331}$	<0.001
Site	$33.6_{1,331}$	<0.001
Age	$0.1_{,331}$	0.74
Year	$51.6_{1,331}$	<0.001
Sex×age	$10.4_{1,331}$	0.002
Age×*Haemoproteus*	$7.2_{1,331}$	0.008
Sex×age×*Haemoproteus*	$3.5_{1,331}$	0.031

Prevalence of *Haemoproteus* blood parasites was related to hue of breast plumage in an age- and sex-dependent manner (Table 1). Both among female and male yearlings, uninfected birds had higher average values of hue than infected birds (Fig. 1). Hue of old females was not related to their infection status, while infected old males had higher values of hue than uninfected ones.

Lutein absorbance

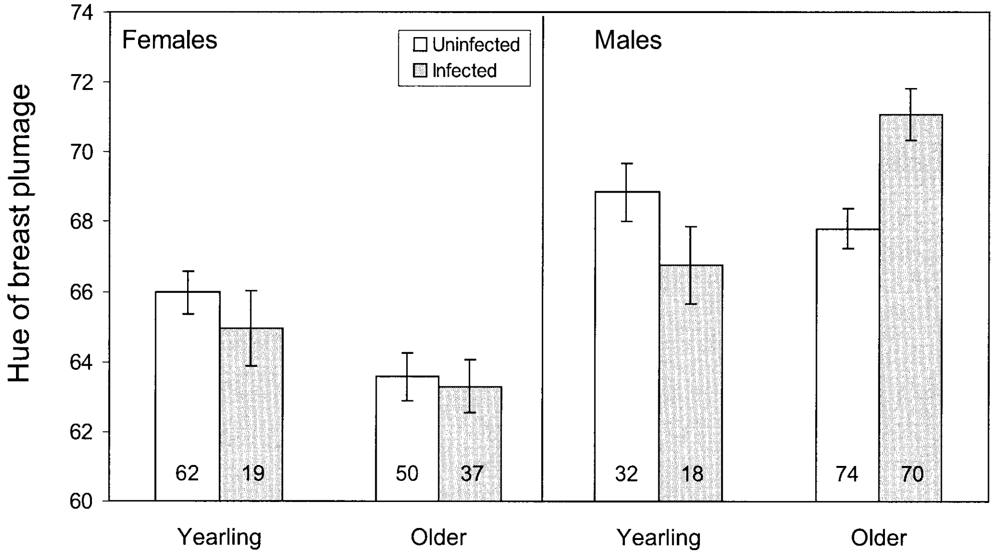
Rural great tits were “more yellow” than urban ones [on average a 5.6% difference; lutein absorbance of rural birds, 0.75 (0.14), *n*=124 vs. urban birds, 0.71 (0.16), *n*=208]. Males and females, as well as age classes, did not reveal consistent differences in respect to lutein absorbance of yellow plumage coloration (see Table 2 for all significance levels). In 1998, the average lutein absorbance was higher [0.84 (0.12); *n*=151] than in 1999 [0.63 (0.12); *n*=181].

Blood parasite infection status had a significant effect on the “yellowness” of plumage colour (Table 2). This relationship was evidently caused by especially high values of lutein absorbance among infected rural birds in 1998 (Fig. 2).

Local survival in relation to plumage colour and infection status

Twenty-five percent of great tits whose plumage colour was measured in 1998 were recaptured as breeders in the following year. Survivors had a significantly higher value of hue [69.2 (5.4)] than non-survivors [66.7 (6.3); on average a difference of 3.7% or a difference of 0.43 SD units, $t_{50,150}$=2.56, *P*=0.011]. We found no evidence that the relationship between plumage hue and local survival varied among bird categories, since all interaction terms between hue and age, sex, habitat and infection status

Fig. 1 Hue of breast plumage in breeding adult great tits in relation to sex, age and *Haemoproteus* prevalence. Data are least square means and SEs, calculated by the SAS GLM procedure; i.e. adjusted values, accounting for the confounding factors (from the model presented in Table 1). *Numbers on bars* denote sample sizes



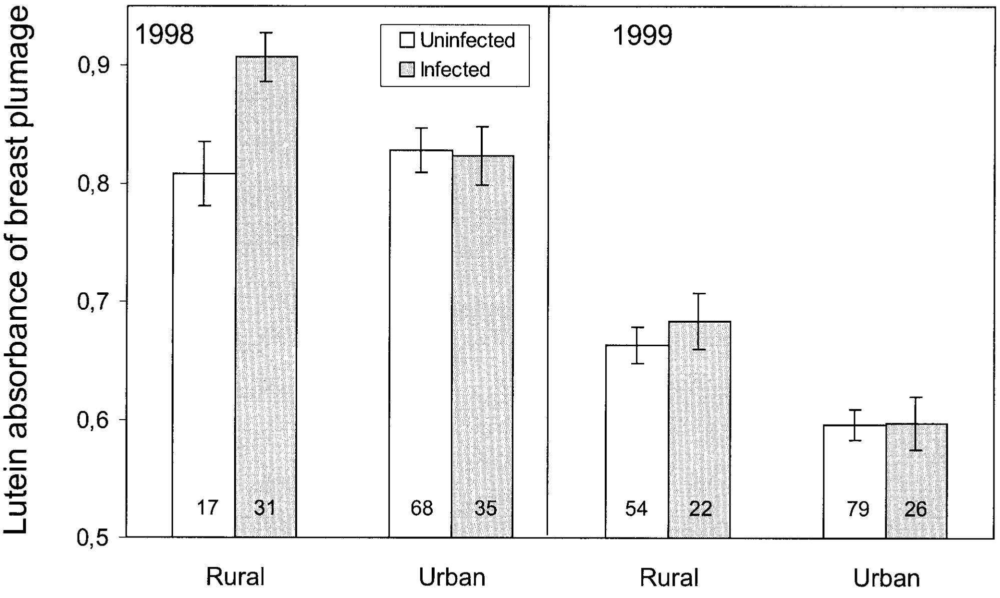


Fig. 2 Lutein absorbance of breast plumage in breeding great tits in relation to year, study site and *Haemoproteus* prevalence. Data are least square means and SEs from the model in Table 2. *Numbers on bars* denote sample sizes

Table 2 Factors affecting lutein absorbance of breast plumage colour in breeding great tits; $R^2=0.51$

Effect	F_{df}	*P*
Haemoproteus	$4.2_{1,331}$	0.041
Sex	$1.0_{1,331}$	0.32
Site	$14.5_{1,331}$	0.002
Age	$0.2_{,331}$	0.65
Year	$212.9_{1,331}$	<0.001
Site×*Haemoproteus*	$4.7_{1,331}$	0.030
Site×year×*Haemoproteus*	$2.0_{1,331}$	0.112

Table 3 Factors affecting local survival of great tits whose blood parasite infection status was measured in 1998 (159 individuals; SAS CATMOD procedure). Probability of likelihood ratio >0.05 indicates that the model fits the data

Effect	*df*	χ^2	*P*
Sex	1	0.21	0.65
Site	1	1.75	0.19
Age	1	0.00	0.99
Haemoproteus	1	0.26	0.61
Age×*Haemoproteus*	1	4.70	0.030
Likelihood ratio	10	10.25	0.41

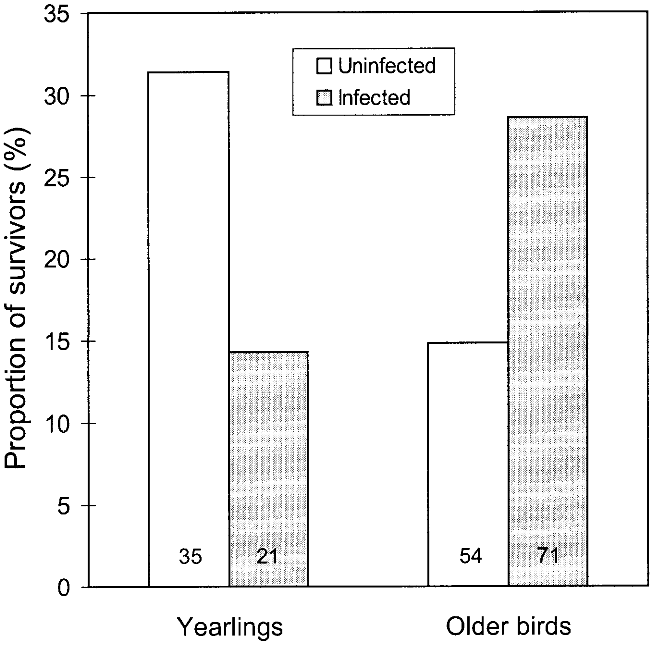


Fig. 3 Local survival and prevalence of *Haemoproteus* in yearling and older great tits. *Numbers on bars* denote sample sizes

turned out to be insignificant in logistic regressions treating local survival as a dependent variable. Lutein absorbance of plumage did not differ significantly between survivors and non-survivors [0.83 (0.13) vs. 0.84 (0.13); $t_{50,150}=-0.89$, $P=0.9$].

Infection status was related to local survival of great tits in an age-dependent manner (Table 3). Non-infected yearlings survived better than infected ones, while the older birds revealed the opposite pattern (Fig. 3). Sex and site differences (Table 3) or their interaction terms with infection status did not affect local survival of great tits (all *P* values <0.3).

Discussion

Our study revealed several distinct patterns in yellow breast plumage coloration of great tits with respect to sex, age, breeding habitat and health status. Of these, the most uniform differences were related to habitat. Great tits breeding in an urban area had lower values of both colour parameters and hence appeared to be "less colourful" or "more drab" than rural conspecifics. These habitat-related differences suggest that urban birds are constrained during moulting by the quality or the quantity of carotenoids available for developing bright and saturated yellow plumage coloration. This constraint may arise from either: (1) low carotenoid content in food items, or (2) greater extent of activation of immune and detoxification processes in urban birds, as compared to rural conspecifics. The first explanation is consistent with the findings of Slagsvold and Lifjeld (1985), showing that great tits reared in deciduous woodland (rich in carotenoid-containing food items) were more yellow than those reared in coniferous woodland, which is a less rich source of carotenoids. Eeva et al. (1998) found that the coloration of great tits breeding along a gradient away from a source of heavy metal pollution was positively correlated with the distance from this source. Since caterpillars were less abundant close to the source of pollution, it is likely that differences in coloration were related to differences in availability of carotenoids (Eeva et al. 1998). There is no experimental evidence of carotenoids limiting the expression of plumage coloration in great tits, but this is not surprising given that carotenoid limitation only has been shown in the field in a couple of studies (Grether et al. 1999; Saino et al. 2000). Our findings are also consistent with the results of Hill (1992, 1993) showing a direct causal relationship between the amount of dietary carotenoids and plumage coloration in house finches (*Carpodacus mexicanus*) in captivity. Furthermore, the limited availability of carotenoids in the urban habitat is supported by a cross-fostering experiment, revealing that great tit hatchlings born in the rural study area, but reared in town, developed less yellow plumage coloration than their siblings reared in the original habitat (Hõrak et al. 2000). The second explanation would imply that the reduction of coloration of urban great tits results from their greater exposure to infectious diseases and/or oxidative stress. However, great tits in our urban study area are characterised by better health status (Ots et al. 1998), lower reproductive effort (Hõrak et al. 1998), and higher survival rates (Hõrak and Lebreton 1998) than rural conspecifics. This does not support the prediction that pale coloration of urban birds resulted from higher depletion of carotenoids due to oxidative stress caused by a higher “rate of living” and energy turnover.

The finding that males on average had (6%) greater values of hue of yellow coloration than females confirms similar results of Slagsvold and Lifjeld (1985) that great tits are sexually dichromatic with respect to carotenoid-based plumage colour. Hence, we might predict that certain components of the yellow coloration of breast plumage in great tits may serve as a target of sexual selection. This prediction requires an experimental test.

Locally surviving individuals had higher values of hue of breast plumage than non-survivors. This result is consistent with the prediction of the Hamilton-Zuk hypothesis that condition-dependent plumage colour reflects individual quality (in terms of future survival prospects). The significant difference in carotenoid-based coloration between local survivors and non-survivors is similar to the difference reported between surviving and non-surviving individuals from a mycoplasma epidemic of house finches (Nolan et al. 1998). More generally, males with more extravagant coloration or other sexual displays consistently have better survival prospects than males with less exaggerated displays across insects, fish, birds and mammals (M. Jennions et al., unpublished data).

The relationships between age-specific infection, immunity and fitness costs of human malaria are far from clear despite extensive research efforts involving thousands of scientists during many decades. Hence, it is not surprising that we know hardly anything about these phenomena in avian malarial infections. Progress has particularly been hampered by an inability to experimentally change the infection status of hosts, which would allow causal relationships to be identified. The negative effects of malaria on survival of avian hosts are particularly severe among young individuals with na immune systems (Atkinson and van Riper 1991). Our study showed that local survival of great tits was related to hemoparasite infection status. The relationship between survival and prevalence of *Haemoproteus* was age-specific: among yearlings, uninfected birds survived better than infected ones, while among older individuals, on the contrary, infected birds survived better than uninfected ones (Fig. 3). Such an age-dependent pattern was also found in a different sample of individuals in the same great tit populations during 1995 and 1996 (Hõrak and Ots 1998). Similarly, studies of the collared flycatcher *Ficedula albicollis* have also shown age-dependent patterns of survival in relation to infection with Haematozoa (Nordling 1998). These results can be explained by the higher virulence of parasites in young, immunologically more na birds. Initial infections often appear deadly, which makes young age classes most susceptible. However, if the host survives, the parasite may enter a chronic phase, where immune responses of the host keep the parasite at a low level with little or no signs of disease (see review in Atkinson and van Riper 1991). Hence, due to selective mortality in young age classes, the cohort of old individuals is expected to contain more individuals with inherited parasite resistance. As a result, old infected individuals may survive better (since they have been proved able to cope with parasites) than uninfected old individuals, which may have escaped encounters with parasites in their previous life stages, and whose immune system, therefore, appears to be untested for resistance to blood parasites.

The relationship between plumage coloration and prevalence of *Haemoproteus* was not straightforward: the relationship between lutein absorbance of plumage and infection status was related to habitat (Fig. 2), while for hue, the relationship depended on age and sex (Fig. 1). These patterns of infection can be interpreted if we know the mechanisms linking parasite infection to carotenoid-based plumage coloration. Many sexually dichromatic birds show clear sex differences in plasma carotenoid levels, with males having higher levels (Hill et al. 1994; Hill 1995; Bortolotti et al. 1996; Figuerola and Gutierrez 1998). This sex difference may relate directly to signalling, but we should also consider the possibility that demands for immune function and detoxification may differ between the sexes (Møller et al. 1998; von Schantz et al. 1999; Møller et al. 2000). We hypothesise that a potential mechanism relating plumage colour to infection status is the trade-off between carotenoid deposition in plumage and anti-parasite immune response (Zuk et al. 1990; Lozano 1994; Skarstein and Folstad 1996; von Schantz et al. 1999; Blount et al. 2000; Møller et al. 2000). Carotenoids that form the yellow pigments of plumage in great tits (Partali et al. 1987; Slagsvold and Lifjeld 1985; Stradi 1998) also affect immune function: lymphocyte proliferation, enhancement of macrophage and cytotoxic T-cell capacities, stimulation of cytokines and interleukins. Furthermore, carotenoids also affect free-radical scavenging (see, for example, review in Møller et al. 2000). It is thus possible that the allocation of carotenoids to immune function or antioxidant activity may reduce the amount of carotenoids available for signals, creating a negative relationship between allocation of carotenoids to plumage and immune defence (Shykoff and Widmer 1996; von Schantz et al. 1999; Blount et al. 2000; Møller et al. 2000). The pattern that old infected males appeared more colourful than uninfected ones can be explained by the same line of arguments. We assume that the cohort of “infected old birds” mainly consists of “immunotolerant” or “resistant” individuals that have proven their ability to cope with infections due to selective mortality caused by *Haemoproteus* (and other) infections in young age classes. We might speculate that the costs of exploiting the immune system (in terms of the allocation of carotenoids to immune defence at the cost of developing signals) are the cheapest in this category of individuals. Although we have currently no correlative or experimental evidence concerning these mechanisms, the assumption that immune responses against *Haemoproteus* are age- and sex-specific is consistent with previously documented age- and sex-specific patterns of relationships between immune parameters and *Haemoproteus* infection status in these great tit populations (Ots and Hõrak 1998).

Surprisingly, the relationship between blood parasites and lutein absorbance was qualitatively different from the relationship between blood parasites and hue described in Fig. 1. Unlike the case of hue, the relationship between lutein absorbance and blood parasites was independent of age, but was related to habitat (Fig. 2), with infected rural birds being the most colourful class of individuals. The simplest interpretation of this pattern is that infected birds in the rural population represent the most immuno-tolerant individuals, signalling their ability to cope with parasites while acquiring and allocating carotenoids to sexual signals. The lack of difference in lutein absorbance between infected and uninfected birds in the urban population could be explained by a lower availability of carotenoid-based food items in the urban habitat (making certain aspects of signals very expensive). Alternatively, it may be explained by differences in patterns of natural selection being related to differences in local parasite faunas between habitats. It is important to note that previous intraspecific tests of the relationship between plumage coloration and Haematozoan infections in birds have yielded inconsistent results, since the predicted negative relationship between parasitemia and expression of secondary sexual traits has been found in some studies (Höglund et al. 1992; Sundberg 1995; Wiehn et al. 1997; Merilä et al. 1999), but not in others (Kirkpatrick et al. 1991; Weatherhead et al. 1993; Seutin 1994; Dufva and Allander 1995; Korpimäki et al. 1995; see Møller et al. 1999 for a review).

In conclusion, sex-, age-, habitat- and disease-related differences in yellow ventral plumage coloration of adult great tits supported predictions of functional hypotheses about the extent of coloration serving as a signal reflecting individual quality. However, these relationships differed among characteristics of colour, suggesting that different aspects of coloration are affected by different physical and biochemical processes and pathways of allocation of dietary carotenoids for development of signals. Furthermore, age-, sex- and habitat-related relationships between plumage coloration and hemoparasite infection indicate the complexity of underlying relationships between selection, environment, disease resistance and function of carotenoids in the expression of sexual signals.

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