INTERACTING EFFECTS OF SIGNALLING BEHAVIOUR, AMBIENT LIGHT AND PLUMAGE COLOUR IN A TEMPERATE BIRD, THE BLUE TIT *PARUS CAERULEUS*

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RÉSUMÉ. — *Interaction des effets du comportement de signalisation, de la lumière ambiante et de la couleur du plumage chez un oiseau tempéré, la Mésange bleue* Parus caeruleus. — Les individus peuvent maximiser leur visibilité par rapport aux congénères tout en minimisant leur probabilité d'être détectés par leurs prédateurs en choisissant le moment et le lieu de leur comportement de signalisation. La visibilité d'un patron de couleur d'un individu est déterminée d'une part par le contraste entre la lumière reflétée par les différents signaux colorés du patron et la lumière reflétée par le fond visuel dans la lumière ambiante où est effectué le comportement de signalisation. Elle est déterminée d'autre part par la capacité de détection de ce contraste par les systèmes visuels des congénères et des prédateurs. Nous avons étudié tout d'abord si différents environnements lumineux peuvent se distinguer dans une forêt tempérée d'un parc urbain, et ensuite si les mâles de Mésange bleue utilisent cette variabilité pour optimiser leur visibilité intraspécifique tout en réduisant la probabilité de détection par les prédateurs. Nous avons mesuré la réflectance des différentes régions du plumage et des fonds visuels, l'irradiance des environnements lumineux disponibles pendant la période de reproduction, et nous avons utilisé les mesures de la sensibilité des photorécepteurs de la Mésange bleue *Parus caeruleus* et ceux d'un oiseau ayant un système visuel similaire à celui de son principal prédateur l'Epervier d'Europe *Accipiter nisus*. Nous avons trouvé des environnements lumineux différents dans le temps et dans l'espace (au cours d'une journée et au long de l'année) que les oiseaux pourraient exploiter et sélectionner pour la signalisation sexuelle. Nous avons trouvé que la couleur de la calotte paraît être plus visible dans l'environnement lumineux aube/crépuscule pour les congénères et prédateurs. Par ailleurs, cette couleur apparaît moins visible dans l'ombre de bois pendant le jour pour les congénères comme pour les prédateurs. Les mâles de Mésange bleue, en se signalant plus intensément à l'aube durant la période de reproduction, optimiseraient la communication intraspécifique sans minimiser leur détectabilité par leurs prédateurs. Au contraire, en choisissant de chanter principalement dans l'ombre de la végétation au cours de la journée, les mâles de Mésange bleue réduisent la probabilité d'une détection visuelle par leurs prédateurs mais aussi leur visibilité aux congénères.

SUMMARY. — Individuals can increase their conspicuousness to conspecifics while minimizing their probability of detection by predators by choosing the time and location of their display. Conspicuousness arises from the contrast between the light reflected by the colour patches, and the light reflected by the visual background in ambient light used for displays. Conspicuousness also depends on the discrimination abilities of both conspecifics and predators. We investigated whether different light environments are present in temperate woodlands, and whether male Blue Tits use this variability to optimize intraspecific conspicuousness while reducing the probability of detection by predators. We measured reflectance of plumage and visual backgrounds, irradiance of available light environments during the breeding period. We used measures of photoreceptor sensitivity of the Blue Tit *Parus caeruleus* and of a bird approaching that of its main predator the European sparrowhawk *Accipiter nisus.* We found different light environments in space and time (during the day and throughout the year) that birds could exploit and select for sexual signalling. The blue crown colour appears to be more conspicuous in early/late light environments but during the day it appears to be least conspicuous in woodland shade for both conspecifics and predators. Male Blue Tits, by displaying more intensively at dawn during the breeding period, would optimize intraspecific communication without minimizing detectability by

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predators. Inversely, by choosing to sing mainly in woodland shade during the day, male Blue Tits reduce the probability of visual detection by predators but also their visibility to conspecifics.

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Animals use visual cues in a wide range of behaviours essential to their survival and reproduction. An animal's conspicuousness is partly determined by its colour. Colour signals are used in intraspecific communication for territory acquisition and defence, mate attraction and mate choice (Andersson, 1994; Bradbury & Vehrencamp, 1998). In the context of sexual selection, they are likely selected by conspecifics for maximum conspicuousness (Endler, 1992). Colour signals are also submitted to interspecific selective pressure leading to aggressive or protective camouflage and are in this context selected for maximum crypsis (Endler, 1978, 1992; Bradbury & Vehrencamp, 1998; Théry & Casas, 2002; Ruxton *et al.*, 2004; Théry *et al.*, 2005). Animal colouration is thus often the result of a trade-off between the antagonistic actions of sexual and natural selection (Endler, 1978, 1980, 1983, 1992; Cummings *et al.*, 2003; Gomez & Théry, 2004).

The conspicuousness of an animal's colour pattern is the contrast between the light reflected by the different colour patches in the pattern and the light reflected by the visual background during colour pattern transmission in a specific light environment (Endler, 1987, 1990; Endler & Théry, 1996; Bradbury & Vehrencamp, 1998). Maximal conspicuousness is achieved for colours which are rich in the wavelengths present in the ambient light and poorly reflected by the visual background (Endler, 1990, 1993). Conspicuousness also depends on the discrimination abilities of the visual systems of both conspecifics and predators (Endler, 1991; Bradbury & Vehrencamp, 1998; Cummings *et al.*, 2003; Théry *et al.*, 2005).

In the tropics, it has been shown that ambient light and visual background are spatially and temporally heterogeneous. Six light environments have been defined in tropical forests: early/late, large gaps, small gaps, woodland shade, forest shade and open/cloudy (Endler, 1993). Individuals of some tropical species have been shown to exploit this heterogeneity by choosing the time and location of their display in order to maximize intraspecific communication while minimizing the risk of being detected by predators (Endler, 1987, 1991; Endler & Théry, 1996; Heindl & Winkler, 2003a, b; Gomez & Théry, 2004; Uy & Endler, 2004). For instance, Endler (1987, 1991) found that male guppies court in locations where visual predation is minimal and use the visually less conspicuous sneak copulation strategy when predation risk is greatest. In some tropical lekking birds, manakins (Endler & Théry, 1996; Heindl & Winkler, 2003a, b) and the Guianan Cock-of-the-rock (Endler & Théry, 1996) males place their lek and/or perform their lek display in the available light environment that maximizes the conspicuousness to potential mates but minimizes detectability by predators (Uy & Endler, 2004). Significant associations between plumage colouration and use of light environments have also been found at the community level in Guianan (Gomez & Théry, 2004) and Australian (McNaught & Owens, 2002) birds. Although similar heterogeneity of light environment has been described in northern American temperate woodlands (Chiao *et al.*, 2000), no study has yet investigated whether temperate species use this heterogeneity while signalling.

In northern Europe, male Blue Tits *Parus caeruleus* sing in deciduous forest subcanopy (Cramp & Perrins, 1993). The singing period begins at the end of winter or beginning of spring in leafless forests and stops in late spring i.e. in forests with complete foliage cover. Singing activity generally peaks at dawn during the fertile period of females but also occurs during the day (Cramp & Perrins, 1993; Caro *et al.*, 2005). Several non-exclusive hypotheses have been put forward to explain the occurrence of a dawn chorus. First, dawn may be especially appropriate because of better acoustic transmission, lower predation, or inefficient foraging at that time (Mace, 1987a; Staicer *et al.*, 1996). Second, the dawn chorus may also result from a non-functional consequence of elevated levels of testosterone that influence song (Staicer *et al.*, 1996). Third, dawn may be the ideal time for sexual selection, because of high male competition pressure (Kacelnik & Krebs, 1983), higher cost after a night without feeding (Mace, 1987a; Staicer *et al.*, 1996) and increased female attention just before copulation (Mace, 1986). Fourth, dawn may offer a visual environment that would enhance conspicuousness to conspecifics while minimizing the detection by predators (Endler, 1978, 1992). Ambient light colour depends on time of day, vegetation geometry, sun angle and the proportion of cloudy sky (Endler, 1993). Different light environments might therefore be available for Blue Tits both at seasonal and daily scales.

The aims of our study are twofold. Primarily, we measured, in northern European temperate woodlands of an urban park, the different types of light environments which were described

by Endler (1993) in tropical forests and by Chiao *et al.* (2000) in northern American forests. Secondly, we tested whether a species known to use colour for intra-sexual (Alonso-Alvarez *et al.*, 2004) and inter-sexual communication (Svensson & Nilsson, 1996; Andersson *et al.*, 1998; Hunt *et al.*, 1998, 1999, 2001; Sheldon *et al.*, 1999, Delhey *et al.*, 2003; Griffith *et al.*, 2003), the Blue Tit, displays preferentially in a light environment which maximizes its conspicuousness to conspecifics and its crypsis to predators. Therefore, we measured the spectral characteristics of male plumage colouration, background colouration during the early and later breeding periods, and the available light environments. We then computed visual contrasts in the Blue Tit visual system (Hart *et al.*, 2000) and in a model developed to approach the one of its avian predator, the European sparrowhawk *Accipiter nisus*. Variations in male Blue Tit signalling behaviour were also investigated in relation to time of day to estimate light environment selection by Blue Tits.

MATERIAL AND METHODS

STUDY SITE AND SPECIES

Fieldwork was carried out in March-May 2004 on a Blue Tit population breeding in nest-boxes in the urban park of the Muséum National d'Histoire Naturelle at Brunoy (2°30'0''E, 48°42'0''N, France). This park is representative of the regional woodlands; its vegetation mainly consists of oaks *Quercus pubescens* and hornbeams *Carpinus betulus*. Leaves appear at the beginning of April and foliage cover is complete by the mid of April. In the population of interest, nest building was observed in March, laying in mid April (March 31 to April 15), incubation at the end of April (April 16 to April 26) and nestlings feeding in May (April 27 to May 29).

SPECTRORADIOMETRY

We measured the irradiance of light environments available during the early breeding period (March-mid April) and when the leaves are present at the mid of April with a portable spectroradiometer (Avantes USB-2000 calibrated between 200-850 nm). The surface of the cosine-corrected irradiance probe (Ocean Optics CC3) pointing upwards collected light at a solid angle of 180° on a surface measuring 6 mm in diameter. The spectroradiometer was calibrated with a light source of known spectral energy distribution (Avantes Avalight DH-CAL). Irradiance data were transformed into photon flux units according to Endler (1990).

Until the appearance of leaves (i.e. all the early breeding period), we took measurement of all light environments that were present. They coincided with what Endler (1993) described as early/late, large gaps, woodland shade and open/cloudy. Large gaps and woodland shade were also similar to what Chiao *et al.* (2000) described in northern American temperate woodlands, although our measurements were extended to ultraviolet wavelengths. Large gaps corresponded to open areas. In woodland shade, a large proportion of blue sky was visible but the sun was not directly visible. When the sky was cloudy, all the day light environments converged towards the spectrum of open/cloudy. The early/late was computed as the mean of five spectra taken on five different days at random points on our study site. Each of five spectra of early/late was the mean of 11 spectra: one spectrum measured at dawn civil time (the sun was at six degree under the horizon) calculated for our study site, five spectra measured five minutes before dawn civil time and five spectra measured five minutes after dawn civil time. The early/late measurements were taken in woodland shade in both open and cloudy sky conditions. We present only the results with the early/late measured under an open cloudy as we found no qualitative difference between open and cloudy sky conditions (Fig. 1). We did not measure the ambient light at dusk; we presumed that it was the same as at dawn. Each spectrum of the other light environments was computed as the mean of five spectra taken during five minutes the same day. When leaves were present (i.e. during the later breeding period), we also measured all light environments present. The same four light environments were identified in the later breeding period as in the early breeding period, but two additional light environments appeared with ambient light filtering by leaves: forest shade and small gaps (Endler, 1993). Contrary to woodland shade, the sky was not visible in forest shade. The small gaps are sunlit locations smaller than 1 m in diameter for a 30 m-high canopy. Spectra of each of these additional light environments were computed as the mean of five spectra taken during five minutes the same day.

We measured background reflectance (bark and foliage) and feather reflectance for four plumage regions (crown, back, throat[*] and belly) with the same spectroradiometer and a deuterium-halogen light source (DH-2000 emitting between 215-1 500 nm) connected with a 1.5 mm diameter sensor inserted in a miniature black chamber (Théry *et al.*, 2005). Reflectance spectra were taken at 90° relative to the surface and relative to a 99% reflectance standard (300-700 nm Spectralon) and to dark current (black felt background). One reference and one dark current calibration were taken before measuring feathers of each individual, each leaf or each bark sample. Feather samples were collected from ten adult males nest-trapped in May whilst feeding nestlings. Four contour feathers were plucked from four plumage regions: blue crown, yellow throat, yellow belly and green back. For each bird and each region, we computed the mean of five reflectance spectra, each measured with four superimposed feathers placed on the non-reflecting black felt.

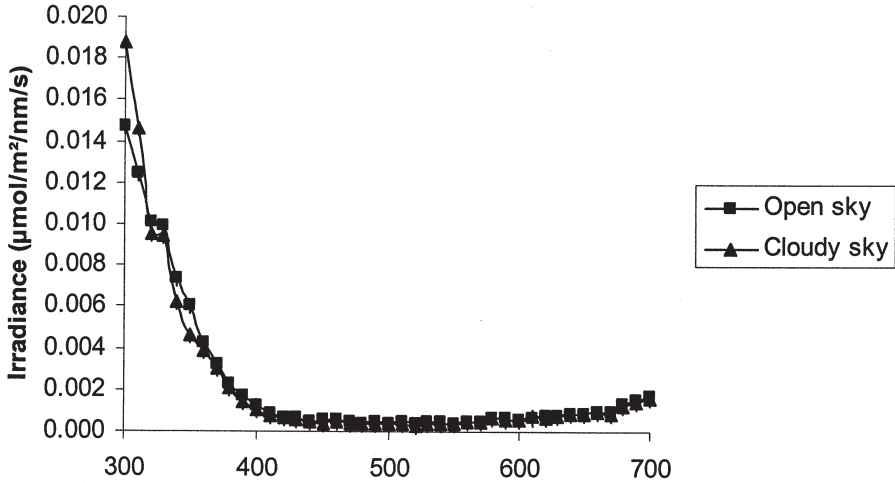[*] For convenience we use here "throat" instead of "upper breast".

Figure 1. — Irradiance spectra (mean ± standard error) of early/late in open and cloudy sky conditions measured during the early breeding period.

Two types of visual background were available for the singing Blue Tits during the study. Bark is the predominant background when Blue Tits acquire and protect their territory and seek or avoid extra-pair copulations (Cramp & Perrins, 1993; Andersson *et al.*, 1998) during nest building and until the end of laying. The bark spectrum was computed as the mean of spectra taken on two samples of each tree species, oak and hornbeam. For each tree species, these spectra were taken on five different points of each bark sample in order to reflect the bark heterogeneity (algae, moss and lichen). When pairs are formed and less sexual selection occurs during incubation, the main background is foliage. The foliage spectrum was computed as the mean of eight leaves spectra of each tree species (oak and hornbeam). For each tree species, these spectra were taken on five different points of each leaf in order to reflect the leaf heterogeneity. Bark and foliage samples were randomly taken in our study site.

MODELLING VISUAL SYSTEMS AND CONTRASTS

To study intraspecific communication, we calculated chromatic and achromatic contrasts as described by Théry *et al.* (2005) with spectral sensitivities of the Blue Tit (Hart *et al.*, 2000). We measured both types of visual contrasts since, even in constant conditions, birds use different signal parameters depending on the size of the target: chromatic aspects of visual signals are important for the detection of large objects, whereas achromatic aspects are important for the detection of small objects (Osorio *et al.*, 1999a, b). Although eye models make no predictions on the relative importance of chromatic and achromatic contrasts, there is indirect evidence that birds primarily communicate using chromatic contrast because avian predators select for reduced chromatic but not achromatic contrasts in prey (Stuart-Fox *et al.*, 2004; Håstad *et al.*, 2005). The study of crypsis and conspicuousness to predators would ideally require the knowledge of the visual sensitivities of the European Sparrowhawk, which is the main tit predator (Perrins & Geer, 1980; Newton, 1986). Although largely unknown, this species is violet-sensitive (peak at 405 nm; Ödeen & Håstad, 2003) like the Wedge-tailed Shearwater *Puffinus pacificus* which has a well-known visual system with a cone sensitive to very short wavelengths (VS) peaking at 406 nm (Hart, 2004). Moreover, Hart (2001) has shown that among violet-sensitive (VS) bird species, the wavelength of maximum absorbance (λ_{max}) of the VS visual pigment is positively correlated with small wavelength-sensible (SWS) visual pigment λ_{max} value. It is therefore important to use a VS species with a λ_{max} around 405 nm in order to get a model of VS and SWS cones representative of Sparrowhawk vision.

We calculated the spectral location of bird plumage regions in the colour space of both Blue Tit and Wedge-tailed Shearwater using estimated responses of the four Blue Tit and Shearwater photoreceptors, taking into account visual pigment absorbance, oil droplet and ocular media transmittances (Hart *et al.*, 2000; Hart, 2001, 2002, 2004).

In the model we used, we consider that cones are adapted to the background and that the estimated response to a stimulus of each cone *i* is:

$$Q_i = \int_{300}^{700} R_{bluetit}(\lambda) \times I(\lambda) \times S_i(\lambda) d\lambda \bigg/ \int_{300}^{700} R_{background}(\lambda) \times I(\lambda) \times S_i(\lambda) d\lambda \qquad (1)$$

Where *i* is the type of photoreceptor (ultraviolet-sensitive UVS or VS, SWS, medium wavelength-sensitive MWS and long wavelength-sensitive LWS), $R_{bluetit}(\lambda)$ is the reflectance spectrum of each body region of Blue Tit plumage, $I(\lambda)$ the irradiance spectrum of the respective light environment, $S_i(\lambda)$ the absorption spectrum of the respective cone, and $R_{background}(\lambda)$ is the reflectance spectrum of background (bark or leaf). Calculation is conducted in the range 300-700 nm.

In order to reflect the saturation of photoreceptor responses, we apply a non-linear correction as following:

$$P_i = Q_i/(Q_i + 1) \qquad (2)$$

Colour sensation arises from the comparison between the responses of the distinct classes of cones, i.e. from the relative differences between cones irrespective of their absolute responses. By normalizing receptor excitations to a given stimulus to the summed responses for that stimulus, we disentangle chromaticity from achromatic intensity. For each cone i, the normalized receptor excitation is:

$$E_i = P_i \bigg/ \sum_i P_i \qquad (3)$$

The relative excitations (E_{UVS}, E_{SWS}, E_{MWS}, E_{LWS}) define a three-dimensional space in which the maximal response of the cones project as the vertices of a colour tetrahedron (Kelber *et al.*, 2003). We thus define a possible set of Euclidean coordinates for this three-dimensional space as:

$$\begin{cases} x = \dfrac{2\sqrt{2}}{3} \times \dfrac{\sqrt{3}}{2} \times \left(E_{MWS} - E_{LWS} \right) \\[2mm] y = E_{UVS} - \dfrac{1}{3} \times \left(E_{SWS} + E_{MWS} + E_{LWS} \right) = 1 - \dfrac{4}{3} \times \left(E_{SWS} + E_{MWS} + E_{LWS} \right) \\[2mm] z = \dfrac{2\sqrt{2}}{3} \times \left(\dfrac{1}{2} \left(E_{MWS} + E_{LWS} \right) - E_{SWS} \right) \end{cases} \qquad (4)$$

In the predator visual system, E_{VS} was used instead of E_{UVS}.

In the chromatic space described above, chromatic contrast against the background (i.e. colour contrast CC) was computed as the Euclidian distance ΔSt separating the background and the reflectance spectrum under consideration:

$$\Delta St = \sqrt{\left(\Delta x\right)^2 + \left(\Delta y\right)^2 + \left(\Delta z\right)^2} \qquad (5)$$

In this model, the background lies at the origin of the colour space and thus produces a null chromatic contrast.

Birds are thought to use double cones to detect achromatic contrast (i.e. brightness contrast; Maier & Bowmaker, 1993; Osorio *et al.*, 1999a, b; Goldsmith & Butler, 2005). When the double cones sensitivity was unknown, combining the absorbance spectra of MWS and LWS photoreceptors is a good approximation of sensitivity of double cones (Hart *et al.*, 2000; Hart, 2001). We thus apply equations (1) and (2) replacing $S_i(\lambda)$ by the sum of the absorbance spectra of cones sensitive to medium and long wavelengths. The achromatic distance between two colours A (colour of one body region of Blue Tit plumage) and B (background colour) represents achromatic contrast AC and is defined by:

$$AC = \sqrt{\left(Pdb_A - Pdb_B\right)^2} = Pdb_A - Pdb_B \qquad (6)$$

In this model, the background has a brightness of 0.5 and the achromatic contrast of a colour A against background is $Pdc_A - 0.5$. Negative values of achromatic contrast indicate that the body region of Blue Tit plumage is darker than the background. Inversely, positive values of achromatic contrast indicate that the body region of Blue Tit plumage is brighter than the background.

The reflectance of different plumage regions was measured on feathers collected during the nestling feeding period and not during pair formation or the breeding period when most sexual selection occurs (Cramp & Perrins, 1993; Andersson *et al.*, 1998). In Blue Tits, Örnborg *et al.* (2002) showed that the amount of ultraviolet/violet crown reflection changes seasonally and is the weaker during the nestling feeding period probably due to fat and dirt accumulation on feathers. Consequently, the modelled contrasts to conspecific and predator visual systems are underestimated in the ultraviolet/violet part of crown spectrum but also for throat, belly and back.

ESTIMATION OF DISCRIMINATION THRESHOLDS

We established discrimination thresholds, i.e. minimal values for chromatic and achromatic contrasts below which visual signals would unlikely be discriminated against the background. This estimate allowed to distinguish biologically relevant results (statistically significant differences in contrast that would be likely discriminated by the avian visual systems tested) from others (statistically significant differences in contrast unlikely detected by a visual system). To our knowledge, colour discrimination as a function of wavelength has only been established for the pigeon *Columbia livia*. For this violet-sensitive species, discrimination is highest in the blue and green-yellow regions (respectively around 450 nm and 540 nm) where two monochromatic colours only differing by 4 nm are perceived as different (Neumeyer, 1991). We assumed that a similar value of 4 nm is also plausible for a ultraviolet-sensitive species like the Blue Tit and that the optimal resolution domain may extend down into the ultraviolet, as shown in the Budgerigar *Melopsittacus undulatus* which possesses a good spectral sensitivity in the UV-blue, green and yellow wavelengths in natural light conditions (Goldsmith & Butler, 2003).

We created a series of spectra based on normal functions (maximal reflectance of 100%, located each 4 nm from 300 to 700 nm, variance of 5 nm) to mimic monochromatic lights separated by this discrimination threshold value found for pigeons. For each spectrum we computed its coordinates in the avian colour space using all possible combinations of background (bark and foliage) and light environments (open/cloudy, early/late, small gaps, large gaps, woodland shade, forest shade) available at the end of the breeding season (i.e. the later breeding period). We then calculated the Euclidean distance separating two spectra differing in their mean by 4 nm (e.g. distance between S300 and S304), obtaining the chromatic contrast and achromatic contrast between these two colours. When the maximal reflectance was located below 328 nm, between 492 and 504 nm and above 644 nm, the spectra generated quantum catches less than 0.05 relative to a 99% white reflectance standard in all four single cones. In that case, photoreceptor responses fall below their noise, i.e. the Weber fraction value of 0.05 commonly chosen for birds (Vorobyev *et al.*, 1998; Håstad *et al.*, 2005). We considered that these colours convey little or no chromatic information and were unlikely processed by colour

vision, following the method established by Osorio *et al.* (2004). We thus excluded these colours from the calculation of distance between pairs of spectra. We obtained discrimination thresholds of 0.055 for chromatic contrast and 0.01 for achromatic contrast.

BIRD OBSERVATIONS

We monitored six nests during the nest building period and 10 nests during the laying and incubation periods. We observed the signalling behaviour of males at these nests throughout the breeding season (March-May 2004) and several times throughout the day. At each breeding stage (nest building, laying, and incubation), we recorded by continuous focal sampling (Altmann, 1974) the signalling behaviour of each of the focal males during the whole chorus at dawn (30 min before dawn civil time until the female exited the nest box; observation duration ≈ 1 h) and dusk (30 min before sunset until 15 min after the female came back in the nest box; observation duration ≈ 1 h) and for 60 min at 9 am, 1 pm and 5 pm. Each time a male sang, we determined in which light environment it performed its song display, the observer being placed at less than 5 m from the bird. Songs were recorded with a Marantz portable cassette recorder PMD 222 at each nesting stage. We calculated total song display time during 60-min sampling periods including pause duration of less than 5 min (pause time between each strophe and between each strophe type or song type; Poesel *et al.*, 2001).

STATISTICAL ANALYSES

We assessed repeatability of chromatic and achromatic contrasts from each plumage region (crown, back, throat and belly) of 10 males computed with the early/late environment. Colour measurements were taken five times for each individual. We found a high repeatability for three of these regions (one-way ANOVA, blue crown: $F_{9,59} > 3.2$, $P < 0.01$, $r > 0.76$; green back: $F_{9,59} > 2.6$, $P < 0.01$, $r > 0.73$; yellow throat: $F_{9,59} > 3.2$, $P < 0.01$, $r > 0.76$) but not for belly which was excluded from the statistical analyses (one-way ANOVA, $F_{9,59} < 2.1$, $P > 0.05$, $r < 0.68$).

For both chromatic and achromatic contrasts, differences between colour patches and between visual systems for a given light environment and period were tested using Kruskal-Wallis test and Mann-Whitney U test respectively. Chromatic and achromatic contrasts were compared between light environments (dependent variables) using the Friedman ANOVA. When significant differences were observed, we used the Wilcoxon Signed Rank test to compare light environments pairwise. These statistical tests were two-tailed and performed with version 9 of Systat (SPSS 1998).

We used generalized linear models (McCullagh & Nelder, 1989) to investigate whether males sing at a particular time of day and stage of the breeding season, and whether they choose a particular light environment to display during the day. Generalized linear models allow us to select an appropriate link function and response probability distribution depending on the data (binomial, multinomial, Poisson). Statistical analyses were performed with Proc Genmod (version SAS 8.2; SAS Institute 2001). We started with the saturated model with binomial distribution and with different times of day as repeated measures and individual as random effects, and subsequently dropped the non-significant terms ($P > 0.05$). A χ^2 test on likelihood ratio was used to test the statistical significance of terms.

RESULTS

LIGHT ENVIRONMENTS PRESENT IN AN URBAN PARK

The light environments measured in our study according to the description made by Endler (1993) are qualitatively different (Fig. 2). There are thus the same number and types of light environments in temperate woodlands than in tropical forests.

COMPARISON OF PLUMAGE CONTRASTS WITHIN WHOLE BODY PATTERN

The blue crown offered a significantly higher chromatic contrast than the yellow throat or the green back in each breeding period and available light environment for conspecifics and predators (Kruskal-Wallis test, $\chi^2 > 4.4$, df = 1, n = 10, $P < 0.04$; Fig. 3 for conspecifics). The green back offered a significantly higher chromatic contrast than the yellow throat in all periods and light environments for conspecifics and predators (Kruskal-Wallis test, $\chi^2 > 4$, df = 1, n = 10, $P < 0.05$; Fig. 3 for conspecifics) except in the early/late environment for conspecifics (Kruskal-Wallis test, $\chi^2 < 1.7$, df = 1, n = 10, $P > 0.19$; Fig. 3 for conspecifics).

For both conspecifics and predators, the blue crown and green back offered a significantly higher achromatic contrast than the yellow throat in each light environment available during the early breeding period (Kruskal-Wallis test, $\chi^2 > 7.8$, df = 1, n = 10, $P < 0.006$; Fig. 4a). During the later breeding period, the yellow throat offered a significantly higher achromatic contrast than the blue crown and green back in each available light environment (Kruskal-Wallis tests, $\chi^2 > 8.6$, df = 1, n = 10, $P < 0.004$; Fig. 4b).

During the early breeding period, the blue crown offered higher chromatic and achromatic contrasts at dawn or dusk than during the day for conspecifics and predators (the magnitude of statistical differences in chromatic contrast — CC — and achromatic contrast — AC — are: CC = 0.004, AC = 0.02 for conspecifics and CC = 0.007, AC = 0.02 for predators; Table I). The green back offered similar chromatic contrast at dawn or dusk than during the day for both conspecifics and predators (Table I). Using achromatic contrast, the green back was more conspicuous at dawn or dusk than during the day for both visual systems (AC = 0.01 for conspecifics and AC = 0.01 for predators; Table I). On the contrary, the yellow throat offered similar chromatic contrast in all light environments for conspecifics but was more visible at dawn or dusk than during the day for predators (CC = 0.02 for predators; Table I). Using achromatic contrast, the yellow throat was less conspicuous at dawn or dusk than during the day for both visual systems (AC = 0.007 for conspecifics and AC = 0.006 for predators; Table I).

TABLE I

Light environment-dependent variations of chromatic and achromatic contrasts for Blue Tits and predators. The magnitude of statistical differences in chromatic and achromatic contrasts found between light environments is in parentheses

| | Chromatic contrast | | | | | | Achromatic contrast | | |
| | Conspecifics | | | Predators | | | Conspecifics and Predators | | |
	Crown	back	throat	crown	back	throat	crown	back	throat
Early breeding period									
Early/late > day or Early/late < day	> ** (0.004)	–	–	> ** (0.007)	–	> * (0.02)	> ** (0.02)	> ** (0.01)	< ** (0.007)
Most conspicuous day light environment	LG **	LG *	–	LG *	WS * (0.004)	WS * (0.002)	LG *	LG **	WS ** (0.002)
Least conspicuous day light environment	WS ** (0.0008)	–	–	WS * (0.0005)	–	–	WS ** (0.007)	WS ** (0.004)	LG **
Later breeding period									
Early/late > day or Early/late < day	< ** (0.009)	–	> * (0.03)	< ** (0.009)	< ** (0.009)	–	> ** (0.01)	> ** (0.02)	> ** (0.02)
Most conspicuous day light environment	FS * (0.002)	FS * (0.001)	FS ** (0.003)	FS ** (0.002)	–	–	LG **	LG **	LG **
Least conspicuous day light environment	WS * (0.001)	WS * (0.0009)	–	–	–	–	FS ** (0.02)	FS ** (0.03)	FS ** (0.03)

FS: forest shade, LG: large gaps; WS: woodland shade.
For each contrast, > (or <) means that the value is significantly higher (or lower) for the early/late environment compared to day light environments.
For all tests, we analyzed the coloration of 10 adult males. When no habitat-light significant difference was obtained from the Friedman-ANOVA (df = 5, n = 10, χ^2 > and P > 0.05) a sign – was figured for all three comparisons (Early/late vs. day, most conspicuous, least conspicuous) concerning one breeding period and contrast.
When any habitat-light significant difference was detected from the Friedman-ANOVA, we performed Wilcoxon signed rank tests (see methods for details). In this case, for each of the three comparisons concerning one breeding period and contrast, we mentioned the level of significance of the Wilcoxon signed rank tests: –: non-significant; *: P < 0.05; **: P ≤ 0.005. The magnitude of statistical differences in chromatic and achromatic contrasts found between light environments allowed to make a comparison with discrimination thresholds of 0.055 for chromatic contrast and 0.01 for achromatic contrast. The early/late environment and large gaps were taken as reference for calculations of the magnitude of differences in chromatic and achromatic contrasts found between light environments.

During the later breeding period, all colour patches offered higher achromatic contrast at dawn or dusk than during the day for both predators and conspecifics (crown: AC = 0.01, back and throat: AC = 0.02 for conspecifics and predators), while it was the contrary for chromatic contrast (crown: CC = 0.009, throat: CC = 0.03 for conspecifics and crown: CC = 0.009, back: CC = 0.009 for predators) except for the back for conspecifics and the throat for predators (back: CC = 0.008 for back and CC = 0.009 for throat), for which no significant difference were detected on chromatic contrast (Table I), and except for throat for conspecifics for which chromatic contrast was greater at dawn or at dusk than during the day (CC = 0.03 for conspecifics; Table I).
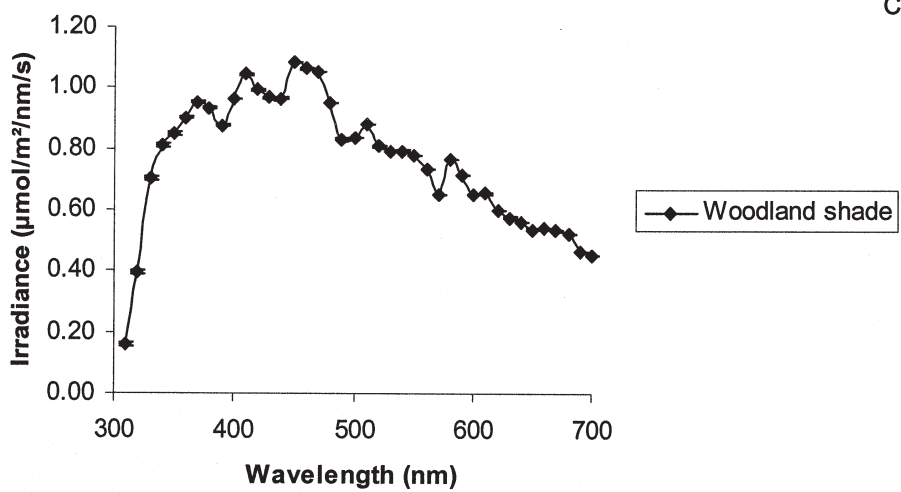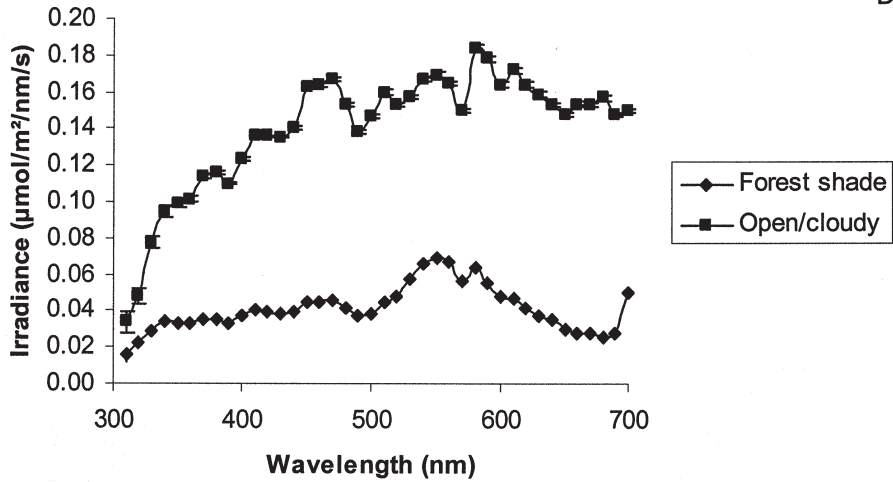
A

B

C

D
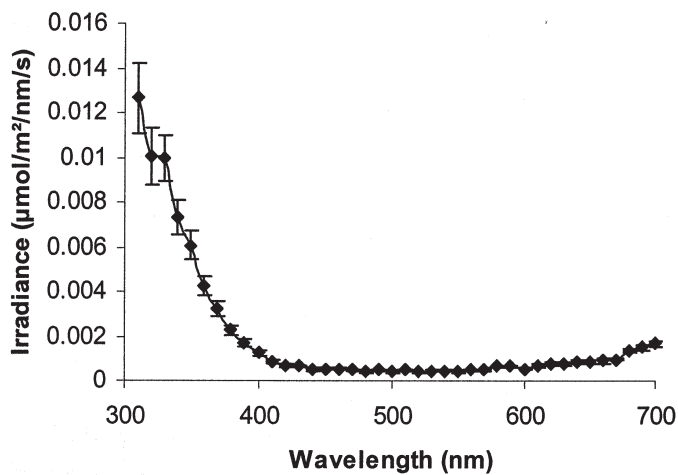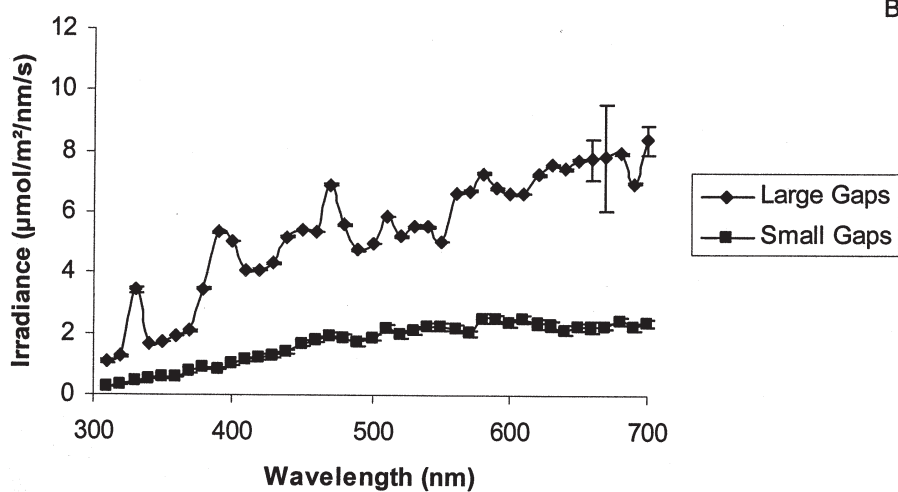
Figure 2. — Irradiance spectra (mean ± standard error) of early/late (A), large and small gaps (B), woodland shade (C) and forest shade and open/cloudy (D) light environments measured during the later breeding period.
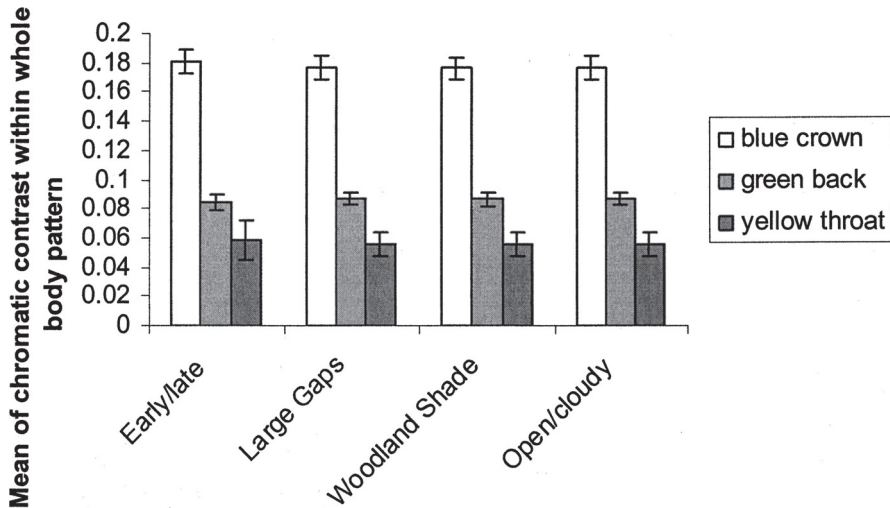

Figure 3. — Mean chromatic contrast (± standard error) of plumage regions within whole body pattern of male Blue Tits, as seen by conspecifics during the early breeding period.

COMPARISON OF PLUMAGE CONTRASTS IN THE DAY LIGHT ENVIRONMENTS FOR CONSPECIFIC AND PREDATOR VISUAL SYSTEMS

Using chromatic and achromatic contrasts during the early breeding period, the blue crown was most conspicuous in large gaps and least conspicuous in woodland shade in both visual systems (the magnitude of statistical differences in chromatic contrast — CC — and achromatic contrast — AC — are: CC = 0.0008, AC = 0.007 for conspecifics and CC = 0.0006, AC = 0.007 for predators; Table I). The green back was most conspicuous using chromatic contrast in large gaps for conspecifics, and in woodland shade for predators (CC = 0.0006 for conspecifics and CC = 0.001 for predators; Table I). Using achromatic contrast, the back was most conspicuous in large gaps and least conspicuous in woodland shade in both visual systems (AC = 0.004 for
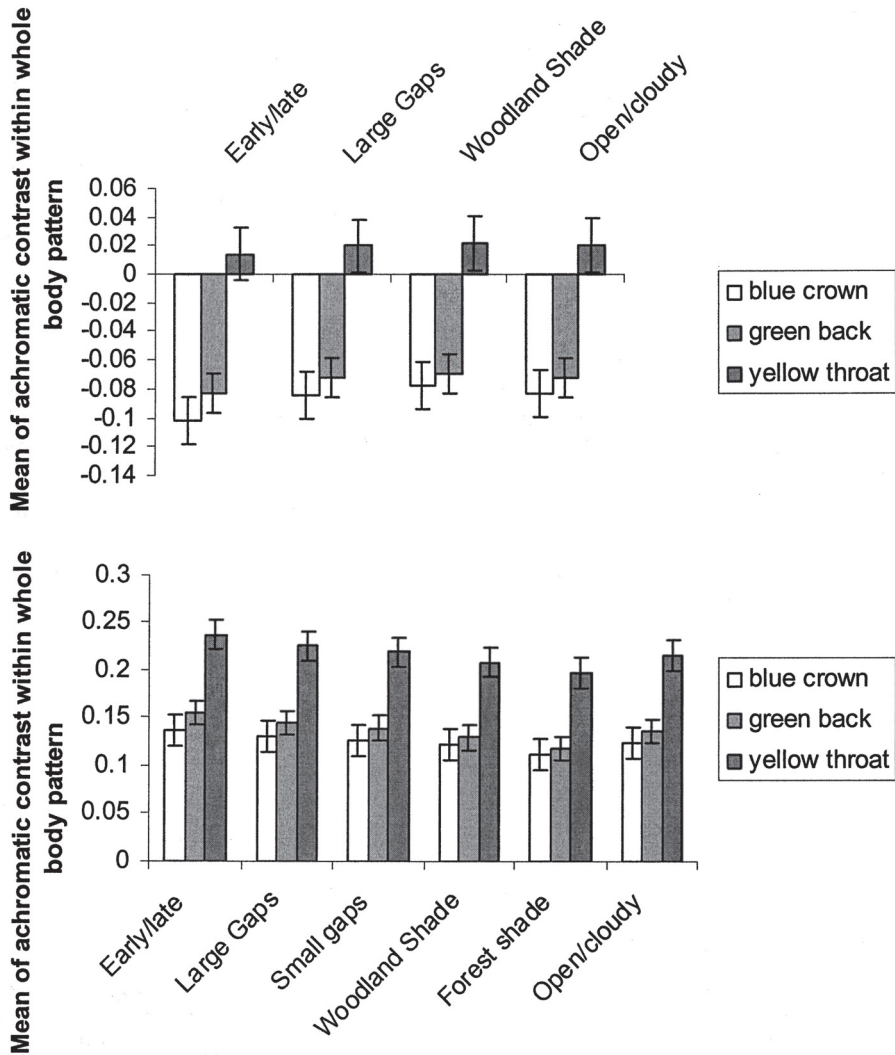
Figure 4. — Mean achromatic contrast (± standard error) of plumage regions within whole body pattern of male Blue Tits, as seen by predators during the early (a) and later breeding periods (b).

conspecifics and predators; Table I). The yellow throat offered similar chromatic contrast in all light environments for conspecifics, but was more conspicuous in woodland shade than in the other day light environments for predators (CC = 0.003 for predators; Table I). Using achromatic contrast, the yellow throat was more conspicuous in woodland shade than in large gaps (AC = 0.002 for conspecifics and predators; Table I).

Using achromatic contrast during the later breeding period, all colour patches were most visible in large gaps and least conspicuous in forest shade, either to conspecifics or to predators (crown: AC = 0.02, back: AC = 0.03; throat: AC = 0.03 for conspecifics and predators; Table I). Using chromatic contrast, forest shade was the light environment where all colour patches were most conspicuous for conspecifics (CC = 0.002 for crown, CC = 0.001 for back and CC = 0.003 for throat; Table I). For predators, only the blue crown was more conspicuous in this light environment (CC = 0.002 for crown; Table I). Woodland shade offered conditions where chromatic contrast was lowest for the blue crown and green back for conspecifics (CC = 0.001 for crown and back), and only for the green back for predators (CC = 0.0008 for back; Table I).

All colour patches offered similar achromatic contrasts for both visual systems over the whole breeding period. Similar chromatic contrast was offered to conspecifics and predators in all light environments for the blue crown over the whole breeding period (Mann-Whitney U test, $\chi^2 < 1.5$, df = 1, n = 10, P > 0.2), and for the yellow throat and green back during the later breeding period (Mann-Whitney U test, the early/late environment: $\chi^2 \approx 3.2$, df = 1, n = 10, P ≈ 0.07 and others light environments: $\chi^2 < 1.4$, df = 1, n = 10, P > 0.24). However, during the early breeding period, the yellow throat and green back presented similar chromatic contrast for conspecifics and predators in the early/late light environment (Mann-Whitney U test, $\chi^2 < 0.04$, df = 1, n = 10, P > 0.8) but were more conspicuous for conspecifics than for predators in all other day light environments (CC = 0.01 for back and CC = 0.02 for throat and for all day light environments; Mann-Whitney U test, $\chi^2 > 5.4$, df = 1, n = 10, P < 0.02).

BEHAVIOUR OF MALE BLUE TITS RELATIVE TO LIGHT ENVIRONMENTS

Males sang more at dawn than during the day or at dusk (Proc Genmod, $\chi^2 = 8.3$, df = 2, P = 0.016; Fig. 5) but did not sing more at a particular time during the day (Proc Genmod, $\chi^2 = 1.65$, df = 2, P = 0.44; Fig. 5). Conversely, males sang more during laying period than during nest-building or incubation (Proc Genmod, $\chi^2 = 3.67$, df = 3, P < 0.0001; Fig. 5).
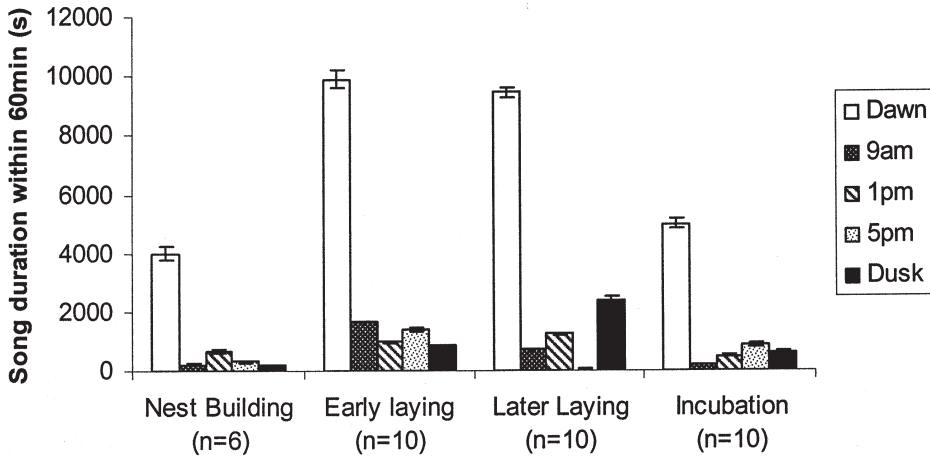

Figure 5. — Mean (± standard error) song duration during continuous 1 hr observation in relation to time of day and breeding stages. To allow comparison, the observation exceeds the duration of dawn, but most singing activity was observed in the early/late light environment.

Males sang more often on clear than on cloudy days (Proc Genmod, $\chi^2 = 7.3$, df = 1, P = 0.0067).

In clear weather conditions, males sang only in two light environments: woodland shade and large gaps. They sang more often in woodland shade than in large gaps (Proc Genmod, $\chi^2 = 8.7$, df = 1, P = 0.0032; Fig. 6).

DISCUSSION

LIGHT ENVIRONMENTS HETEROGENEITY

We found that temperate woodlands of an urban park can potentially offer a complexity of light environments similar to that of tropical forests (Endler, 1993), particularly when their foliage cover is fully developed as after mid April. These results are also consistent with the study of Chiao *et al.* (2000), although we went further by measuring ambient light at dawn and when
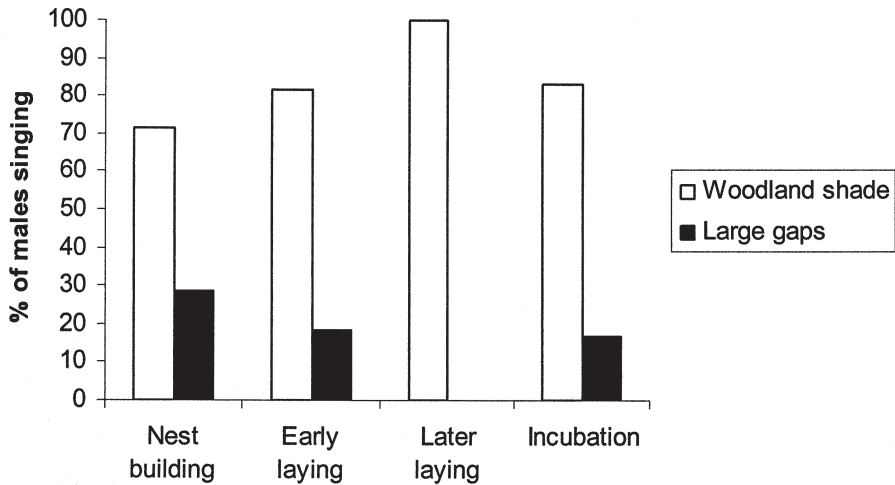
Figure 6. — Percentage of males singing in large gaps or woodland shade during day displays.

the sky is covered by clouds and by taking into account the UV part of ambient light spectrum (300-400 nm). However, compared to evergreen rainforests, temperate forests rich in oak and hornbeams showed higher temporal variation in light environment availability. Loss of foliage cover in autumn was accompanied by a loss of light environment diversity, with forest shade and small gaps being absent in winter and at the beginning of spring. Temperate forests thus offered conditions variable in space and time (during the day and throughout the year) that animals could exploit and select for sexual signalling. Furthermore, temperate woodlands likely constitute a good model for studies investigating light environment selection by birds.

PLUMAGE CONTRASTS WITHIN WHOLE BODY PATTERN

Our results showed that compared to the back or the throat, the blue crown offers higher conspicuousness (chromatic and achromatic contrasts) to both conspecifics and predators during the early breeding period when most sexual selection occurs (Cramp & Perrins, 1993; Andersson *et al.*, 1998) although the modelled crown contrasts are underestimated (see Material and methods). Blue tits display their crown in agonistic and sexual interactions by horizontal 'head-forward'postures with erected nape feathers (Stokes, 1960). Moreover, Blue Tits are sexually dichromatic in their UV-reflecting crown (Andersson *et al.*, 1998; Hunt *et al.*, 1998) and previous studies have suggested that the UV-blue crown is an indicator of male quality used in intraspecific communication (Sheldon *et al.*, 1999; Griffith *et al.*, 2003). Males and females prefer to mate with a strongly UV-reflecting partner (Hunt *et al.*, 1999). Females paired with brighter males have a brood sex ratio biased towards males (Svensson & Nilsson, 1996; Sheldon *et al.*, 1999; Griffith *et al.*, 2003 but see Ewen *et al.*, 2004). The colour of the male blue crown also seems to influence extra-pair copulations (Delhey *et al.*, 2003). Lastly, UV-reflectance of the crown affects male-male interactions (Alonso-Alvarez *et al.*, 2004). Our results showing that the UV-blue crown is the most conspicuous region of the male Blue Tit could thus explain why this colour signal is more extensively used than others for intraspecific communication in this species. The fact that this signal is also easily seen by predators involves costs as a higher risk of predation. Can male Blue Tits counterbalance this cost by choosing the place of sexual signalling?

COMPARISON OF PLUMAGE CONTRASTS IN THE DIFFERENT LIGHT ENVIRONMENTS FOR BOTH CONSPECIFIC AND PREDATOR VISUAL SYSTEMS

Under natural light environments, the strongest stimulus power is in the achromatic contrast (Vorobyev & Osorio, 1998) and long-distance communication and detection of moving targets, either prey or predators, likely involve achromatic vision (Osorio *et al.*, 1999a, b; Spaethe *et al.*, 2001). In our studied species, primary use of achromatic contrast is reinforced by (1) the comparison of the magnitude of differences in visual contrasts with discrimination thresholds of 0.055 for chromatic contrast and 0.01 for achromatic contrast. This suggested that only differ-

ences in achromatic contrast are likely biologically relevant to both conspecifics and predators (mean differences of 0.01, similar order of magnitude as the discrimination threshold of 0.01). (2) Behavioural observations. During the whole breeding season, we found that male Blue Tits sang more often at dawn than during the day or at dusk. Blue Tits are territorial (Dhondt *et al.*, 1982; Cramp & Perrins, 1993) and at dawn mostly sing close to the nest hole of their roosting mate (Mace, 1987b). Intra-sexual communication between neighbours at dawn may be a long-distance process using achromatic contrast. Furthermore, at dawn, the female is mostly laying inside the cavity and thus cannot see its male. Long-distance conspicuousness of males may be important at dawn for territory defence against floaters (Kacelnik & Krebs, 1983; Amrhein *et al.*, 2004; Kunc *et al.*, 2005; Poesel & Dabelsteen, 2005). Moreover, we found that male Blue Tits sang more during the laying period when males seek or avoid extra-pair copulations (Cramp & Perrins, 1993; Andersson *et al.*, 1998) showing the male song and colour signals may have as functions to protect their social mates against extra-pair copulations and to attract females for extra-pair copulations.

Our results showed that during the breeding season, the levels of long-distance conspicuousness using achromatic contrast vary with the light environments for each plumage region. In the early breeding period when most sexual selection occurs (Cramp & Perrins, 1993; Andersson *et al.*, 1998), the UV-blue crown presented stronger achromatic contrast in the early/late environment than in the day light environments for both predators and conspecifics. In the later breeding period when little sexual selection occurs (Andersson *et al.*, 1998), the UV-blue crown showed higher achromatic contrast in the early/late environment than in the day light environments for either predator or conspecific. Our results may thus suggest that male Blue Tits maximize intraspecific communication during the whole breeding season without minimizing the risk of being detected by predators by displaying mainly in the early/late light environment. However, other evolutionary pressures may also play an important role in determining the time of display. For instance, dawn may constitute a better environment for transmission of acoustic signals to conspecifics (Mace, 1987a; Staicer *et al.*, 1996) and thus for territory defence against floaters (Kacelnik & Krebs, 1983; Amrhein *et al.*, 2004; Kunc *et al.*, 2005; Poesel & Dabelsteen, 2005). In conclusion, dawn and the early/late light environment would allow better transmission of both acoustic and colour signals to conspecifics.

During the day and the whole breeding season, we found that males more often sang in woodland shade than in large gaps. In the early breeding period, the UV-blue crown presented stronger achromatic contrast in large gaps than in woodland shade for both predators and conspecifics. In the later breeding period, the UV-blue crown showed higher achromatic contrast in large gaps than in forest shade for either a predator or a conspecific. By choosing to display mainly in woodland shade, male Blue Tits may not optimize intraspecific communication mediated by colour signals. However, the probability of detectability by predators is minimized even if male Blue Tits do not display in the most cryptic light environment. Alternatively, male Blue Tits may sing preferentially in woodland shade than in large gaps because this habitat may be beneficial for acoustic transmission because at long distance the acoustic signals would be better transmitted in the forest subcanopy (Catchpole & Slater, 1995). During the day, by displaying mainly in woodland shade, communication with conspecifics would be optimized by song. Another explanation is that song perches exposed to woodland shade are most abundant and closest to the nests around which Blue Tits principally seek food during the day (Cramp & Perrins, 1993; Isenmann, 1996).

COMPARISON OF PLUMAGE CONTRASTS IN THE CONSPECIFIC AND PREDATOR VISUAL SYSTEMS

As Håstad *et al.* (2005), we found that the yellow chest of Blue Tits (similar in colouration to the yellow throat) offered in average (considering all possible backgrounds) higher chromatic contrast to conspecifics than to predators. In addition, by separating the different backgrounds according to their availability in time, we found that the yellow throat was more conspicuous for conspecifics than predators only when seen against bark but not against foliage. Similar results were obtained for the green back. Applying the criterion established by Håstad *et al.* (2005), we would have concluded that the yellow throat and the green back were potential signals for conspecifics in the early but not in the later breeding period. Yet the back is often considered as a patch more exposed to predators than to conspecifics (Trail, 1987 for tropical birds; Roth II & Lima, 2003 for temperate birds) and our study shows a much lower potential for the yellow throat than for the blue crown to be used in signalling to conspecifics. Considering the intra-spe-

cific level and replacing the signals in their context of display offer an important complementary view to understand the evolution of colour signals in animals.

CONCLUSION

Male Blue Tits use partly but not optimally the available light environment diversity during their displays. They maximize intraspecific communication without minimizing the risk of being detected by predators by displaying mainly in the early/late environment than during the day. Conversely, by choosing to display mainly in woodland shade during the day, male Blue Tits reduce the probability of visual detection by predators but reduce also intraspecific communication.

ACKNOWLEDGEMENTS

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