Feather ornaments are dynamic traits in the Great Tit *Parus major*

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In behavioural studies it has been common to quantify plumage colours or ornaments over a range of dates and link them to fitness characteristics without accounting for seasonal changes in these traits. Such changes are likely to be widespread among birds, yet we lack assessments of this variability within individuals. We studied both within- and between-individual temporal changes in Great Tit *Parus major* ornaments, specifically the melanin-based black breast stripe and the pigment-free white cheek patch. During the non-breeding season both ornaments varied. In juveniles and adult females, the area of the breast stripe first rose and then, from near the end of December, decreased. In adult males there was a linear decrease. In the cheek patch, the irregularity of the cheek borders showed either a linear (adults) or a non-linear (juveniles) increase as the season progressed. In individuals repeatedly sampled during the same winter, the decrease in the size of the breast stripe was larger for males than females and there was an overall decrease in the regularity of the cheek borders. There was no relationship between the size of the breast stripe and the white cheek patch irregularities or the cheek patch area. These results imply that more attention should be paid to quantification, within individuals, of the components of expression of phenotypic traits. In addition, we suggest that further research should focus on explaining the causes and functions of ornament change.

Keywords: immaculateness, plumage wear, seasonal changes, sexual selection, signalling.

Due to wear, damaged feathers have to be regularly replaced by moult. The newly grown plumage of some birds has distinctly rich and saturated colours which often fade over time (Örnborg *et al.* 2002, McGraw & Hill 2004, Figuerola & Senar 2005, Delhey *et al.* 2006). In others, the nuptial plumage is revealed by feather wear, at the time when mating takes place. Such gradual changes in plumage ornaments have been known for some time in those species such as sparrows and finches where there is a sharp contrast in post-moult and pre-breeding plumage (Newton 1972, Bogliani & Brangi 1990, Møller & Erritzøe 1992, Jenni & Winkler 1994, Veiga 1996, Willoughby *et al.* 2002). However, such changes are likely to be more widespread among birds, even though quantitative assessments are lacking for most species. Instead, it has been common in behavioural studies to quantify plumage colours or ornaments over a range of dates and relate them to fitness traits without accounting for seasonal changes (McGraw & Hill 2004). In addition, models of sexual selection traditionally treat signals (e.g. plumage) as static traits (Andersson 1994). Only recently, it has been emphasized that addressing both spatial and temporal variability in the expression of phenotypes can lead to a better understanding of phenotypic evolution (Cornwallis & Uller 2009).

Here, we focused on quantifying seasonal changes, both at individual and at population levels, in two plumage ornaments, the melanin-based black breast stripe and the pigment-free white cheek patch, in the Great Tit *Parus major*.

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Both traits have been identified as bearers of information on social dominance and reproductive performance (Maynard Smith & Harper 1988, Norris 1990, Ferns & Hinsley 2004, Galván & Sanz 2009a, Galván 2010), so they have a high signal value.

METHODS

This study was carried out between October and March 2004–2008 at six trapping sites in eastern Czech Republic (49°50′N, 17°15′E). Birds were captured by mist-netting at feeders filled with sunflower seeds. The feeders were empty most of the time but were usually filled 2 days before intensive bird trapping.

At each site we trapped birds once every 2 weeks. During the first week of December and the second week of February we carried out more intensive trapping (see details below). We ringed and measured all birds. On a subsample of birds, depending on winter weather conditions, we photographed, with a digital camera (Panasonic DMC-FZ3), the black breast stripe and the left and right white cheek patches. When taking the pictures, birds were held by the bill and legs beside graph paper from a standardized distance. For documenting and measuring the breast stripes we followed the field protocol of Figuerola and Senar (2000), and for the cheek patches, the protocol of Ferns and Hinsley (2004). All photographs were taken by one person (P.A.). Images were analysed with IMAGE J (a freeware available at http://rsb.info.nih.gov/ij/). The outline of each ornament was manually traced by one author (M.V.) and the area or perimeter was measured after calibrating each photograph with a standard from the graph paper. The repeatability of measurements on birds that were recaptured and photographed at least 2 h later on the same day was very high for both breast stripe ($r = 0.98$, $F_{10,11} = 160.71$, $P < 0.001$) and cheek patches (left cheek $r = 0.92$, $F_{10,11} = 33.42$, $P < 0.001$; right cheek $r = 0.94$, $F_{10,11} = 34.56$, $P < 0.001$).

For the left and right cheek patches we used the residuals from an ordinary least-squares regression of the perimeter on area using first captures only. The sex and age of birds had no significant effect in improving model fit and were therefore not included. The left and right residuals for each bird were then averaged and we used this as an index of cheek raggedness. Positive residuals indicate birds with irregular borders, in other words those with high perimeter per unit cheek area (Otter & Ratcliffe 1999, Ferns & Hinsley 2004). To evaluate the seasonal changes in cheek patch area and perimeter, we averaged the values for the left and right cheeks of each bird.

Dates on which the photographs were taken were transformed into days from 1 November (= day 1). We used general linear models (GLMs) to analyse variation in the two studied ornaments. We started with models which included year, sex and age (juvenile vs. adult) as categorical fixed effects and date (linear and quadratic terms) and tarsus length (a surrogate for body size) as covariates. Site was initially fitted as a random effect in a mixed model formulation, but its effect was minimal, and hence the model was simplified to a GLM. We removed non-significant terms at $\alpha = 0.1$ from the model, stopping at the minimum adequate model. Each individual was included only once in the analysis. For those birds that were sampled on several occasions we randomly chose photographs from 1 day only. However, to compare the seasonal change in the two ornaments within the same individuals, each year we carried out intensive daily mist-netting during the first week of December and the second week of February. Birds that were captured on both occasions (mean interval between successive recaptures: 62 days) were photographed and the change in ornaments within the individual was tested by a paired *t*-test. All tests were carried out using JMP 7 (SAS Institute, Cary, NC, USA). In addition, we calculated effect sizes as Cohen's *d* coefficients for categorical predictors and as Pearson's *r* for continuous predictors. Effect sizes from the general linear models were calculated from the corresponding *F*-values using METACALC (Rosenberg *et al.* 2000). Due to the escape of some individuals during the handling process, sample sizes for breast stripes and cheek patches differed. Unless otherwise stated, results are presented as the least-square means (LSM) ± standard errors from particular models.

RESULTS

After controlling for the positive effect of body size ($F_{1,469} = 6.93$, $P = 0.009$, Pearson's $r = 0.12$), the size of the black breast stripe was influenced by age ($F_{1,469} = 9.45$, $P = 0.002$, $d = 0.28$) and sex ($F_{1,469} = 463.34$, $P < 0.001$, $d = 1.99$). The size of the black breast stripe was largest in adult males (means ± se: 838 ± 19 mm^2, $n = 72$), followed by

juvenile males (788 ± 11 mm^2, $n = 208$), adult females (480 ± 19 mm^2, $n = 56$) and juvenile females (434 ± 9 mm^2, $n = 137$). Over the sampling period, the size of the breast stripe significantly declined in adult males ($b = -0.988 \pm 0.493$, $F_{1,69} = 4.01$, $P = 0.049$, $r = 0.23$; Fig. 1) but it first rose and then declined in both juvenile males ($b^2 = -0.028 \pm 0.010$, $F_{1,204} = 7.27$, $P = 0.007$, $r = 0.19$; $b = 0.773 \pm 0.471$, $F = 2.68$, $P = 0.103$) and juvenile females ($b^2 = -0.021 \pm 0.008$, $F_{1,133} = 7.93$, $P = 0.006$, $r = 0.24$; $b = 0.530 \pm 0.347$, $F = 2.32$, $P = 0.129$), and there was also a tendency for such a rising and falling pattern in adult females ($b^2 = -0.032 \pm 0.017$, $F_{1,52} = 3.48$, $P = 0.067$, $r = 0.25$; $b = 0.702 \pm 0.714$, $F = 0.96$, $P = 0.330$; all models contained tarsus length as a covariate). Seasonal change in breast stripe was also found within repeatedly sampled individuals, between early December and mid February (mean interval: 62 days). However, this within-individual change was highly sex-specific ($F_{1,28} = 4.71$, $P = 0.039$, $d = 0.82$). In all males the size of the breast stripe decreased on average by 117 ± 29 mm^2 ($n = 20$), whereas in all females there was no detectable change (decrease by 7 ± 41 mm^2, $n = 10$).

The raggedness of the white cheek patch tended to be higher in juveniles than in adults ($F_{1,359} = 3.19$, $P = 0.074$, $d = 0.19$; juveniles: 0.25 ± 0.31, $n = 247$, adults: −0.72 ± 0.45, $n = 115$). There was no sex effect on this trait ($F_{1,359} = 0.002$, $P = 0.968$, $d < 0.01$) In adults the ra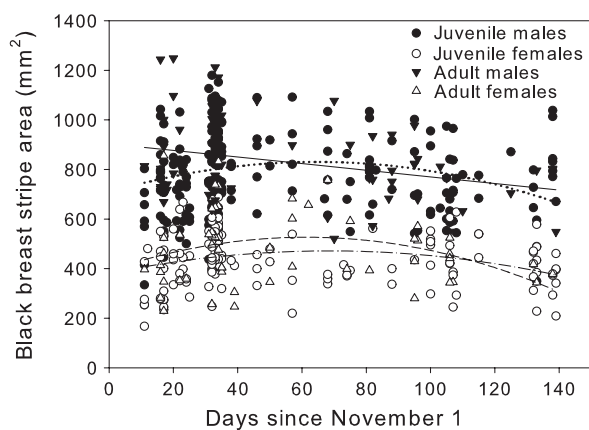ggedness increased linearly over the study period ($b = 0.034 \pm 0.011$, $F_{1,113} = 8.98$, $P = 0.003$, $r = 0.27$), whereas in juveniles it changed non-linearly (quadratic effect of day: $b^2 = -0.00068 \pm 0.00021$, $F_{1,244} = 10.31$, $P = 0.001$, $r = 0.20$; $b = 0.040 \pm 0.007$, $F = 26.52$, $P < 0.001$; Fig. 2). Individuals sampled repeatedly in early December and mid February increased their cheek patch raggedness by 1.88 (95% CI: 0.02–3.75; paired t-test, $t = -2.14$, $P = 0.048$, $n = 16$, $d = 1.11$). When split by age class these data for resampled individuals showed no significant difference ($F_{1,14} = 1.27$, $P = 0.278$, $d = 0.60$; adults 0.43 ± 1.76, $n = 4$, juveniles 2.73 ± 1.02, $n = 12$) but the medium effect size (note the small sample size for adults) indicates that the higher increase in cheek raggedness in juveniles may be biologically relevant.

Females had significantly larger cheek patch areas compared with males (females: 274.8 ± 2.8 mm^2, $n = 146$; males: 258.4 ± 2.4 mm^2, $n = 216$; $F_{1,359} = 21.41$, $P < 0.001$, $d = 0.49$) and adults had significantly larger cheek patch areas than juveniles (adults: 272.1 ± 3.1 mm^2, $n = 115$; juveniles: 261.1 ± 2.1 mm^2, $n = 247$; $F_{1,359} = 8.75$, $P = 0.003$, $d = 0.31$). There was no significant effect of date on this trait. The perimeter of the cheek patch was larger in females than males (females: 79.3 ± 0.6 mm; males: 76.6 ± 0.5 mm; $F_{1,360} = 12.38$, $P < 0.001$, $d = 0.37$). In males, there was a non-linear change in this trait (quadratic effect of day: $b^2 = -0.0010 \pm 0.0003$, $F_{1,213} = 9.81$, $P = 0.002$, $r = 0.21$, $b = 0.053 \pm 0.013$, $F = 17.51$, $P < 0.001$). In females there
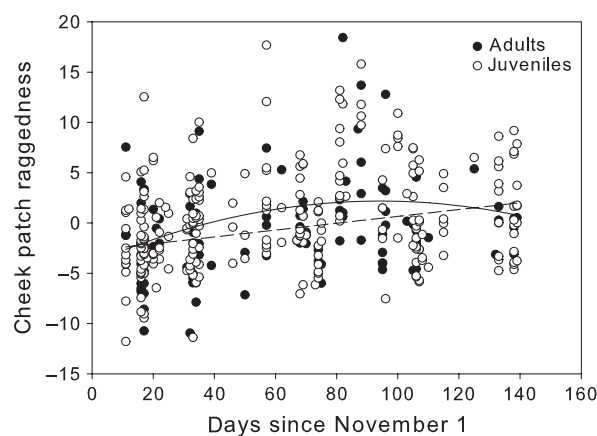

Figure 1. Temporal change of size (area in mm^2) of the black breast stripe in the Great Tit. Overlaid regression lines: solid line – adult males, dotted line – juvenile males, short-dashed line – adult females, dash-dotted line – juvenile females.

Figure 2. Temporal change in the raggedness (averaged residuals for left and right cheek from regression of perimeter on area) of the white cheek patch. Overlaid regression lines: solid line – juveniles, dashed line – adults.

was only a tendency, with a small effect size, for linear increase ($b = 0.027 \pm 0.015$, $F_{1,144} = 3.17$, $P = 0.077$, $r = 0.15$).

There was no relationship between the size of the breast stripe and the white cheek patch raggedness ($r = 0.019$, $P = 0.720$, $n = 355$) or cheek patch area ($r = -0.082$, $P = 0.355$, $n = 355$).

DISCUSSION

We found that both the melanin-based breast stripe and the pigment-free-based white cheek patch are dynamic traits in Great Tits. In juveniles and adult females the size of the breast stripe first increased and then, from near the end of December, decreased, whereas in adult males there was a linear decrease. At an individual level, however, the change in the size of this trait was sex-specific; in males the breast stripe area decreased considerably, but in females there was no change. Cheek patch raggedness showed a slow but steady increase as the season progressed in both adults (linear) and juveniles (non-linear). This pattern was also confirmed for recaptured individuals with some indication of a more pronounced increase in raggedness for juveniles. As the perimeter, but not the size, of the cheek patch changed with date, we found that this was the main reason for the increase in cheek patch raggedness. This supports the idea that an increase in the number of irregularities at the interface of the white cheek patch and the black head feathers is responsible for less immaculate cheeks at the end of the winter. Hence, the temporal variation in expression of these two traits, which may act as signals of dominance (Järvi *et al.* 1987, Maynard Smith & Harper 1988, Ferns & Hinsley 2004, Galván & Sanz 2009b, but see Sandell & Smith 1991, Wilson 1992), needs to be considered in avian studies which deal with feather ornaments. Traditionally, many studies in which plumage has been measured across a longer time span than in this study have treated feather ornaments as static traits. However, a growing number of studies, including this one, highlight that seasonal variation in expression of plumage should not be neglected. In titmice, the available studies provide evidence that colours of ornaments show strong seasonal variation (Örnborg *et al.* 2002, Figuerola & Senar 2005, Delhey *et al.* 2006). In a Hungarian population of Great Tits, the size of the breast stripe increased from October to November (Hegyi *et al.* 2007), a

result which accords with our non-linear temporal pattern for this trait in juveniles and adult females. However, Ferns and Hinsley (2004) did not find significant changes in either the cheek patch immaculateness or the breast stripe width during the winter in recaptured individuals ($d = 0.57$ for the cheek patch and 0.02 for the breast stripe calculated from their test statistics) in a study of British Great Tits *Parus major newtoni*. At a population level, however, they found a temporal increase in cheek immaculateness associated with the apparent loss of less immaculate individuals from the population. The differences in results between continental and British birds might be a consequence of population differences in the information content of the feather traits (Dunn *et al.* 2008, Galván & Moreno 2009).

There might be multiple reasons for the temporal changes in the expression of plumage traits. Progressive accumulation of dirt and fat can reduce the expression of colours (Surmacki & Nowakowski 2007). Similarly, sunlight irradiation, ectoparasites, abrasion or physical attacks with conspecifics can impair the structure of the feathers (Jenni & Winkler 1994, Goldstein *et al.* 2004, Blanco *et al.* 2005). In our case of the seasonal decrease in cheek patch immaculateness, we do not know the proximate mechanism behind this change, but the outcome is that, towards the breeding season, the cheeks of the birds have less immaculate edges. In addition, when compared with adults, juveniles had a higher number of irregularities in their cheek patches. Head feathers usually moult in September (Flegg & Cox 1969), at a time which coincides with autumnal dispersal and territory settlement (Gosler 1993). Hence, for juveniles it might be challenging to allocate resources to both moulting and territory establishment. As a result, juveniles may grow fewer high-quality feathers than adults.

The seasonal change in the size of the black breast stripe shows a slightly different pattern. Apart from in adult males, the size of the breast stripe first increased and than declined. While an explanation for the decline seems straightforward (i.e. caused by the natural abrasion of feathers), the apparent early-winter increase in juveniles and adult females is puzzling. Our large sample size and the similar finding reported for the Hungarian Great Tit population (Hegyi *et al.* 2007) suggest that this increase is not a sampling anomaly. A careful examination of museum skins shows that breast feathers at the border of the black stripe

and lateral yellow patches have a composite structure. Many of the feathers consist of irregular yellow and black parts which are interwoven. If the black melanin-based feather parts are more resistant to abrasion compared with the yellow carotenoid-based parts (Bonser 1995) differential feather wear could lead to a non-linear pattern of ornament change. Another possibility would be differential mortality throughout the winter. At a population level, the mean breast stripe area would increase throughout the winter if less dominant individuals with smaller stripes die preferentially. The mid-winter rising trends for females and juvenile males seem to be in line with this, but not the later falling trend nor the linear decline in adult males. In any case, we suggest that further research should focus on explaining the mechanism of ornament change and its possible adaptive function. The latter seems to be crucial, as it would be very helpful to know how selection based on feather traits changes over the year. For example, overwinter seasonal changes in ornaments might not be important if these traits are under selection only during mating in spring. Similarly, these traits might undergo multiple periods of selection (e.g. late-summer dispersal, mid-winter dominance hierarchy or spring mate choice) and targeting them seems to be a challenging task for future studies.

As already emphasized by McGraw and Hill (2004), in behavioural studies it is quite common to quantify plumage colours or ornaments over a range of dates without accounting for seasonal changes in these traits. Although there is evidence that some of the traits show high individual consistency between successive moults or prolonged time periods (Badyaev & Duckworth 2003, Senar & Quesada 2006, but see Ferns & Hinsley 2004), we argue that a lack of prior quantification of temporal variability in ornamental traits in any focal species might easily lead to confounded results. A true relationship, for example, between some fitness-related trait and plumage might be missed if temporal variation in the expression of a given trait exists. An ideal approach seems to be a combination of quantifying short-term variability with long-term individual consistency in the expression of studied traits (Pérez-Rodríguez 2008).

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