Absolute and relative signals: a comparison between melanin- and carotenoid-based patches

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Summary
Some signalling traits may be highly influenced by environmental factors, thereby decreasing between-year trait repeatability what could compromise the honesty of signal. However, although the repeatability of environmentally-influenced traits of individuals between years may be low, their relative position within the population can be maintained (i.e. significant correlation between years). In the great tit Parus major, individual hue of the yellow breast coloration, an environmentally influenced trait, showed a significant correlation between years in spite of repeatability between years being very low. However, the size of the black breast band, a heritable trait, showed both a high correlation and inter-year repeatability. Results emphasise the distinction between absolute and relative signals and also suggest that for environmentally-influenced ornaments, individuals maintain their relative position on a continuum.

Keywords: signalling, plumage colour, sexual selection, melanin, carotenes, Parus major.

Introduction
Models of sexual selection have traditionally considered that the expression of signals should be constant over time as a consequence of gene expression (Andersson, 1994; Jennions et al., 1995). However, it has recently been
shown that environmental conditions influence the expression of sexual selected traits (Jia et al., 2000; Greenfield & Rodriguez, 2004). In birds, for instance, the absolute value of some sexual traits may change from one year to the next (Pärt & Qvarnström, 1997; Hill, 2002). This should potentially confound the receiver about the honesty of the emitter’s advertisement. Nevertheless, traits may still be reliable in such circumstances provided they either reflect the current status or changes in status over time (e.g., parasite load, physical condition: Qvarnström, 2001; Greenfield & Rodriguez, 2004), or maintain the relative value among the different individuals over time. Thus, the most ornamented individuals in the population in one year would continue to be the most ornamented over the following years, even though environmental conditions may change the medium value of the population trait (Senar et al., 2002). Such data are scarce for birds.

In this paper we use the great tit *Parus major* to test whether environmentally-influenced ornaments in birds (e.g., carotenoid-based hue of the yellow on the breast: Slagsvold & Lifjeld, 1985) can maintain their relative value over time, thereby sustaining the honesty of the signal in spite of the changes in their absolute values. We compare this kind of ornament with that of a highly genetically-influenced trait (the melanin-based black breast stripe: Norris, 1993). We hypothesize that the black stripe operates as an ‘absolute signal’, and predict a high repeatability and correlation between consecutive years in its size, meanwhile the hue of the yellow on the breast functions as a ‘relative signal’, and predict a low inter-year repeatability but a significant correlation in the value of this trait between subsequent years.

**Material and methods**

The study was carried out from 1998 to 2001 in a population of great tits in Northeast Spain. Birds were captured in special funnel traps. Two measures of each trait were taken from the same individual in consecutive years (1 year ± 4 months). We used only adult male birds in the analyses (Euring ages 7 and 9) because: (1) sexual traits and sexual selection are stronger in males than in females (Andersson, 1994), (2) moult is complete in adult birds but only partial in juveniles, (3) both the size of the black breast stripe and the hue of the yellow breast differ between yearling and adult birds (Senar et al., 2003), and (4) senescence could affect plumage coloration of older individuals (Potti & Montalvo, 1991; Møller & De Lope, 1999),
The area of the black breast stripe ($N = 14$) was measured from digital pictures using ImageTool 1.28© (Texas, USA) (Figuerola & Senar, 2000). Mean of the yellow hue coloration of the breast and abdomen was assessed by a portable colorimeter Minolta CR200 (Minolta Corporation 1994©) (Figuerola et al., 1999) ($N = 35$). The great tit presents a peak of UV in the yellow breast plumage but a high correlation between the reflectance of the peak of UV (300-400 nm) and the peak of the yellow-red spectrum (500-700 nm) is present (Spearman rank order correlation, $r_s = 0.83$, $p < 0.001$; $N = 29$, birds measured with Ocean Optics spectrophotometer).

Inter-year repeatability in character expression was measured with one-way ANOVA, according to Lessells & Boag (1987). Inter-year correlation in the expression of the different colour traits was computed with an independent one way-ANCOVA for each trait (melanin and carotenoid hue). ‘1st year’ (1998-2000) was the independent factor which allowed to standardise for yearly variations in ornament expression, ‘ornament value 1st year’ was the dependent variable and ‘ornament value 2nd year’ was the covariant.

**Results**

The hue of the yellow breast colour showed very low inter-year repeatability ($r_i = -0.01$, $p = 0.52$, $N = 35$), but the values of an individual in the population from one year to the next were significantly correlated (ANCOVA, $F_{(1,34)} = 30.77$; $p < 0.001$; covariant interaction: $r = 0.58$, $p < 0.001$, $N = 35$). The greenest male one year thus tended to be the greenest male the following year, thereby maintaining the relative value of each individual in relation to the others in the population (Figure 1).

The size of the great tit black breast stripe showed both a high repeatability in consecutive years ($r_i = 0.76$, $p < 0.001$, $N = 14$), and a high correlation from one year to the next (ANCOVA, $F_{(1,10)} = 2.6$; $p = 0.12$; covariant interaction: $r = 0.91$, $p < 0.001$, $N = 14$).

**Discussion**

Phenotypic plasticity is increasingly recognised to shape character evolution (DeWitt et al., 1998; Payne & Krakauer, 2000; Agrawal, 2001; Price et al.,
For instance, both context-dependent sexual advertisement (Qvarnström, 2001; Badyaev & Qvarnström, 2002; Badyaev & Duckworth, 2003; Badyaev & Young, 2004) and life-history (Griffith, 2000; Qvarnström, 2001) affect ornament expression in birds. However, not all plasticity is adaptive. Passive plasticity, in which variation in character expression is just the result of a response to environmental variation (Scheiner, 1999), may also modulate ornaments. This random variation in character expression could evidently compromise the use of these characters in inter-sexual signalling. Nevertheless, these highly environmental-influenced ornaments may still transmit important information on the qualities of the bearer as long as the relative value of the character of each individual within the population is maintained (Senar et al., 2002). Here we suggest that this is the case for the hue of carotenoid-pigmented great tit plumage coloration. Repeatability of this character from year to year was very low, but the most ornamented individuals one year continued to be the most ornamented in the following years (Senar et al., 2002). This is why we propose calling such characters ‘relative signals’. This would counterpoise to ‘absolute signals’ which to a larger extent would be genet-
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ically determined and show a high repeatability in the expression of their absolute values from year to year (e.g., the black breast stripe).

The relative nature of carotenoid-based ornaments could explain why females from populations with a depressed expression of this character continue to choose very highly ornamented males (Hill, 1994, 2002). Since the expression of carotenoid-based colours can vary both temporally and geographically, the best evolutionary response for females is to be constantly sensitive to the most ornamented males.

What we present as relative and absolute signals are the extremes of a continuum as a very heritable signal may show fluctuations in its absolute value from year to year (Potti, 1993; Griffith & Sheldon, 2001; Qvarnström, 2001; Fitze & Richner, 2002) and a genetic predisposition could also determine a limitation of carotenoid based-colour expression (Tschirren et al., 2003). However, we would like to stress that the concept of the relative value of signals may provide an alternative view to interpret evolutionary processes related to signalling.

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References


