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Dynamics of multiple sexual signals in relation to climatic conditions

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ABSTRACT

Question: Can trait-specific phenotypic plasticity in response to annual environmental variation lead to changes in the strength of sexual selection through the relative expression of sexual ornaments at the population level?

Data description: We recorded breeding dates and the sizes of white forehead and wing patches of male collared flycatchers (*Ficedula albicollis*) from 1998 to 2005 in a nestbox-breeding population in the Pilis Mountains, Hungary. As environmental predictors, we used the North Atlantic Oscillation (NAO) index and local weather data, classified as direct or indirect effects relative to the moult of the given ornament.

Search method: First, we used general linear mixed models to assess environmental effects on the within-individual changes and absolute yearly sizes of forehead and wing patches. We then used similar models to determine whether the relative sizes of the two plumage traits at the population level varied among years. Finally, we used multiple regressions to establish if the relative yearly expression of an ornament affected standardized sexual selection gradients on this ornament in the given year.

Conclusions: Within-individual changes in forehead and wing patch size were predicted by the climate of their moulting season (winter and summer, respectively). There was also an indirect effect of previous winter climate on changes in wing patch size. Environmental effects on the absolute expression of ornaments at the population level followed the within-individual patterns. The relative population-level expression of forehead and wing patches fluctuated significantly among years. Sexual selection on a given ornament increased with its relative expression in that year.

Keywords: collared flycatcher, condition-dependence, *Ficedula albicollis*,
North Atlantic Oscillation, phenotypic plasticity, plumage ornament, sexual selection.

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INTRODUCTION

The expression of conspicuous, sexually selected traits is very frequently linked to the body condition of their bearer (Tomkins *et al.*, 2004), because condition-dependence may prevent the depletion of additive genetic variance (Rowe and Houle, 1996; Wilkinson and Taper, 1999) or mating with individuals of good body condition may confer both direct benefits (Linville *et al.*, 1998) and indirect, genetic advantages (Hasselquist *et al.*, 1996) to females. Sexual selection involves multiple ornamental traits in several species (Candolin, 2003). The relative information content and the co-evolution of multiple sexual signals are poorly understood topics (Badyaev *et al.*, 2002; Saino *et al.*, 2003; Blows *et al.*, 2004).

There are various reports of drastic environmental effects on sexually selected plumage signals, including nuclear radiation (Møller and Mousseau, 2003), environmental pollution (Eeva *et al.*, 1998), and changes in food composition (Linville and Breitwisch, 1997). The effects of yearly climatic or food availability changes on ornamentation may also represent important pieces of information. By studying these effects, the condition-dependence of signals can be assessed with a greater statistical power than with other methods (e.g. Gustafsson *et al.*, 1995; Veiga and Puerta, 1996; Jones *et al.*, 2000; Keyser and Hill, 2000; Johnsen *et al.*, 2003), because the magnitude of the effect is often large, its direction unpredictable, and it affects many individuals in the same way. In addition, if different signals are influenced differently by environmental conditions, this may lead to intriguing interactions between the environment, patterns of sexual trait expression, and sexual selection.

Seasonal environmental effects may be classified as direct or indirect. Direct effects are defined as those that influence trait development in the respective season. Indirect effects, on the other hand, are the long-term influences of particularly stressful conditions, or environments encountered during demanding phases of the life cycle, on sexual signals. In contrast to the descriptions of directional changes in ornament size (Coltman *et al.*, 2003; Møller and Szép, 2005), there are very few reports of yearly fluctuations in the expression of sexually selected traits (Evans, 1991; Jones *et al.*, 2000). Moreover, although sexual signals are known to react to large-scale environmental effects (e.g. Garant *et al.*, 2004; Saino *et al.*, 2004a), the interplay of multiple environmental effects in determining the expression of multiple ornaments has rarely been examined. Consequently, it is unknown how environmental effects restricted to specific signals modify the relative expression of signal traits at the population level, and potentially the relative strength of sexual selection on these traits through sensory exploitation or sexually antagonistic co-evolution (Holland and Rice, 1998).

The collared flycatcher, *Ficedula albicollis*, is an ideal study species for examining these questions. Males have conspicuous, sexually selected white patches on the forehead and the wing that have been subject to long-term studies in two populations (reviewed in Garant *et al.*, 2004; Hegyi *et al.*, 2006). Analyses in a Hungarian collared flycatcher population suggested that the proximate determination of the size of forehead and wing patches differed, with wing patch size exhibiting higher condition-dependence than forehead patch size (Hegyi *et al.*, 2002; Török *et al.*, 2003). Studies on a Swedish population of the species, including correlations with the winter North Atlantic Oscillation (NAO) index, indicated an opposite pattern, with plasticity in forehead patch size but not wing patch size (Gustafsson *et al.*, 1995; Sheldon and Ellegren, 1999; Garant *et al.*, 2004). Forehead and wing patches are developed at different times of the year, and on different continents (Cramp and Perrins, 1993), so different environmental factors specific to year and season may affect the two traits.

Here we examine the plasticity and absolute yearly sizes of forehead and wing patches in a long-term data set from the Hungarian population, using multiple large-scale and local environmental variables that represent potential direct and indirect environmental effects relative to the moulting times of the respective plumage signal. We also quantify the magnitude of fluctuations in yearly relative trait sizes and their consequences for sexual selection. First, we look for relationships between climate and the within-individual changes of signals in males that bred on our plots in two consecutive years. Second, we examine whether climate alters the absolute yearly expression of ornaments, due to either within-individual changes or the differential mortality or movements of individuals, and whether the relative expression of the two ornaments at the population level varies among years. Finally, to determine whether differential climatic effects influence sexual selection via the population-level expression of ornaments, we assess the effect of yearly relative trait expression on the relative strength of breeding date selection on the two traits in the given year.

Beyond illuminating the potential role of large-scale environmental sensitivity in multiple signal evolution, our results may also clarify whether the relative phenotypic plasticity of forehead and wing patches indeed differs between the Hungarian and the Swedish populations (Török *et al.*, 2003; Garant *et al.*, 2004; Hegyi *et al.*, 2006). Such a difference would constitute evidence for rapid evolutionary changes in the information content of signals, given that the two populations separated only after the last glaciation (Sætre *et al.*, 2001). Rapid changes in information content have implications for both the general design and evolution of multiple signal systems (Wiens, 2001; Candolin, 2003), and the recent controversy on whether the metabolic basis of plumage colours predicts their information content (Parker *et al.*, 2003; McGraw, 2005; Poston *et al.*, 2005).

MATERIALS AND METHODS

Field methods

The collared flycatcher is a long-distance migratory, insectivorous, hole-nesting passerine with a pronounced sexual dichromatism (Gustafsson, 1989; Cramp and Perrins, 1993). Males are black and white, with conspicuous white patches on the forehead and wings. A breeding population of collared flycatchers in the Pilis Mountains, Hungary, has been studied continuously since the early 1980s. The study area comprises several plots with a total of more than 800 nest-boxes (for further details, see Török and Tóth, 1988). We caught some males during courtship, but most of them in the second half of the nestling period. We ringed them and took standard measurements of morphological traits as well as ornament sizes. We determined binary age (yearling or adult) from the colour of remiges (Svensson, 1992). We measured the maximum height and width of the forehead patch, as well as the visible lengths of white (i.e. from the respective covert) on the outer vanes of primaries 4–8 with a caliper (to the nearest 0.1 mm). We quantified forehead patch size as the product of height and width (Hegyi *et al.*, 2002, 2006), and wing patch size as the sum of the measured white segments (Török *et al.*, 2003). Measurement repeatability is moderately high and comparable for the two traits [forehead patch: 0.68 ± 0.14 (Hegyi *et al.*, 2002); wing patch: 0.83 ± 0.07 (Török *et al.*, 2003) (mean ± standard error)], so it is unlikely to affect the results. Systematic differences between measurers were corrected for based on average patch size values taken in the same seasons (Hegyi *et al.*, 2006). The males used in the present study were measured in at least one breeding season from 1998 to 2005. The analyses are therefore based on 1611 captures of 1086 males. However, forehead and wing patches were not measured in the case of physical damage to the plumage of the forehead or ongoing primary moult, respectively, so sample sizes vary among tests.

Climatic variables

The two plumage signals are replaced at different times of the year. The forehead patch appears when males emerge from their female-like cryptic plumage in late winter. Wing patches, on the other hand, are renewed during the complete post-breeding moult in summer (Cramp and Perrins, 1993). The exact locations where the moult takes place are uncertain in both cases, since the complete summer moult may overlap with migration, while the partial winter moult usually occurs at the poorly known wintering areas in sub-Saharan Africa (Cramp and Perrins, 1993). In addition to direct influences during moult, we also aimed to assess indirect environmental effects on the two ornaments. Such effects have been suggested for the Swedish population in the context of reproductive costs (Gustafsson *et al.*, 1995), but have not yet been examined in relation to climate. The predictors we used were data on local temperature and precipitation at the study area, as well as the NAO index.

The NAO is an alternating movement of atmospheric masses between subtropical Atlantic and Arctic areas, which exerts large-scale effects on temperature and precipitation patterns on continents bordering the North Atlantic (Hurrell, 1995). The NAO is usually measured by differences in sea level air pressures between pairs of stations in the Mediterranean/Atlantic and the Arctic regions. It is strongest during the winter season, but present throughout the year (for further details, see Stenseth *et al.*, 2003). The NAO has been shown to predict several measures of within-species life-history variation in birds, including arrival date at the breeding grounds (Saino *et al.*, 2004b), breeding success (Møller, 2002), individual survival (Grosbois and Thompson, 2005), and population sizes (Sæther *et al.*, 2003). Moreover, it has been proposed that climatic indices may be generally better predictors of population-level processes than local environmental variables, because they capture a complex co-variation among potentially several components of the environment (Hallett *et al.*, 2004).

In our analyses of ornament changes, we distinguished between indirect and direct climatic effects, and took into account the phenology of moult. We assessed the winter NAO (December to March) preceding the moults of the ornaments as a potential indirect influence on the development of both ornaments through the spring breeding conditions and reproductive costs on our plots in Europe (Przybylo *et al.*, 2000; Møller, 2002). Costs of reproduction, in turn, have been shown to influence subsequent ornament expression in this (Gustafsson *et al.*, 1995) and other species (Griffith, 2000; Siefferman and Hill, 2005). Direct climatic effects during the post-breeding moult of wing patches in June to August were characterized by both local weather conditions at the study area in these months, and the summer NAO index. The summer NAO was used to avoid false-negative conclusions on environmental effects if birds moult their wing patches after leaving the study area. The summer NAO has been shown repeatedly to correlate with European weather (Lindholm *et al.*, 2001; Zveryaev, 2004). Finally, the winter NAO index was used also as a direct climatic effect on the moult of the forehead patch at the wintering grounds in Africa (McHugh and Rogers, 2001; Oba *et al.*, 2001). We summarize the proposed direct and indirect climatic effects in Table 1. We used the modified NAO index of Jones *et al.* (1997), obtained from http://www.cru.uea.ac.uk/cru/data/nao.htm. This index reflects a normalized pressure difference between Gibraltar in southernmost

Table 1. Direct and indirect climatic effects on the change and absolute expression of wing and forehead patches

	Change, yearling	Change, adult	Absolute size, yearling	Absolute size, adult
WPS direct	Summer after breeding as a yearling	Summer after breeding as an adult	Summer after birth	Summer before breeding as an adult
WPS indirect	Winter before breeding as a yearling	Winter before breeding as an adult	Winter before birth	Winter, more than a year before breeding as an adult
FPS direct	Winter after breeding as a yearling	Winter after breeding as an adult	Winter after birth	Winter, a few months before breeding as an adult
FPS indirect	Winter before breeding as a yearling	Winter before breeding as an adult	Winter before birth	Winter, more than a year before breeding as an adult

Note: WPS = wing patch size; FPS = forehead patch size.

Iberia and a composite of sites in south-western Iceland. Monthly mean temperatures and monthly cumulative precipitation were measured by the State Meteorological Service in Budapest, approximately 30 km from the study area. We used the yearly averages of three months (June, July, and August) for these weather variables.

Statistical analyses

General linear mixed models with Satterthwaite correction were employed as implemented in the MIXED procedure of SAS v.8.02 (SAS Institute, Inc.). In the analyses of within-individual changes in sexual ornaments, we used measurement pairs taken from the same bird in two consecutive years. We entered ornament size in the second year as a dependent variable, ornament size in the first year as well as direct and indirect climatic effects as covariates, male identity and year as random factors, and binary age (yearling or older) in the first year as a fixed factor. We also evaluated the two-way interactions of age with climatic effects. Climatic effects for forehead patch size were first winter NAO (indirect effect) and second winter NAO (direct effect). Climatic effects for wing patch size were first winter NAO (indirect effect), first summer NAO (direct effect), and first summer temperature and precipitation (direct effects). In the analyses of absolute ornament sizes, we used ornament size as a dependent variable, climatic effects as covariates, male identity and year as random factors, and binary age as a fixed factor. We also assessed the two-way interactions of age with climatic effects. Climatic effects for forehead patch size were previous winter NAO (indirect effect) and current winter NAO (direct effect). Climatic effects for wing patch size were previous winter NAO (indirect effect), previous summer NAO (direct effect), and previous summer temperature and precipitation (direct effects).

We also conducted an analysis to determine whether the relative expression of the two white plumage signals varied among years. In this test, we used all ornament measurements ($n = 3055$), which were standardized for binary age. This standardization was done separately for the two ornaments, to account for their different age-dependence (Hegyi *et al.*, 2002; Török *et al.*, 2003). The model included standard ornament size as a dependent variable, year, ornament and their interaction as fixed effects, and male identity as a random effect. In the absence of data on extra-pair paternity, sexual selection on the two plumage traits was evaluated based on mating advantage, indicated by breeding date (Hegyi *et al.*, 2006).

Our final aim was to establish if the relative expression of a trait affects sexual selection on it. Relative expression was calculated as the difference between the yearly mean standardized size of the focal trait and that of the other trait. Yearly standardized sexual selection gradients (Arnold and Wade, 1984) were calculated in multiple regressions with binary breeding date (laying of the first egg, before or at the yearly median vs. after the median) as a dependent variable and age- and year-standardized patch sizes as predictors (see also Hegyi *et al.*, 2006). Then, before correlating relative trait expression and sexual selection, we considered a potential confounding factor. Sexual selection on multiple traits may vary in parallel among years due to, for example, year-specific migratory arrival patterns that influence the general potential for mate choice regardless of the trait in question (Lundberg and Alatalo, 1992). Such similarity in selection gradients may make it difficult to interpret the relationship of relative trait expression with sexual selection. In our case, yearly breeding date selection gradients for the forehead and the wing patch were highly positively correlated ($r = 0.795$, $P = 0.018$, $n = 8$). Therefore, to take into account the selective background that acted similarly on the two traits, we fitted multiple regressions with breeding date selection gradient on the focal trait as a dependent variable and the relative expression of the trait as a predictor, and used the breeding date selection gradient on the other trait as a second predictor.

We applied backward stepwise model selection. Non-significant interactions and main effects were sequentially removed, starting with the highest order, least significant terms. Removed terms were then re-entered to the final model one by one to check their significance. The final model included all significant independent variables and interactions, as well as predictors that were not significant themselves, but were involved in a significant interaction. The significance values reported for removed terms refer to their re-introduction to the final model. Temporal trends could confound our results if ornamentation or climate changed directionally during the period covered by our study. However, neither patch size changes nor climatic indices showed such trends (mixed models and correlations respectively, results not shown). Furthermore, pairwise correlations among the climatic variables we entered to the same models were also non-significant during the period we considered ($r < 0.467$, $P > 0.243$, $n = 8$), so multicollinearity does not hamper the interpretation of our results. All analyses were two-tailed. We present means with their standard errors.

RESULTS

Within-individual changes in ornamentation

Change in wing patch size (Table 2) was positively related to first summer NAO (Fig. 1a) and first summer precipitation, and negatively related to first winter NAO, but unrelated to first summer temperature. A significant interaction with age showed that the effect of the first winter NAO was significant in yearling birds ($F_{1,101} = 4.16$, $P = 0.044$), but not in adults

Table 2. Age-specific relationships between indices of year quality and the subsequent changes in white wing patch size within individual collared flycatcher males

	F	d.f.	Estimate	Standard error
Binary age in first year	543.61***	1,420	237.27	10.18
Wing patch size in first year	929.57***	1,420	0.86	0.03
Summer NAO in first year	33.36***	1,420	38.04	6.59
Winter NAO in first year	10.21**	1,420	−3.62	3.26
Summer precipitation in first year	11.90***	1,420	0.33	0.10
Summer temperature in first year	0.44	1,419	1.54	2.31
Age × summer NAO	0.11	1,419	4.65	13.89
Age × winter NAO	4.48*	1,420	−13.49	6.37
Age × summer precipitation	0.74	1,419	−0.17	0.20
Age × summer temperature	0.20	1,418	2.04	4.60

Note: Linear mixed models with backward stepwise model selection. Results for the random factors of male and year (both non-significant) are not shown here. NAO = North Atlantic Oscillation.

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

($F_{1,316} = 1.46$, $P = 0.228$). The graphical inspection of changes in wing patch size in relation to precipitation strongly suggested a non-linear effect. When replacing the linear effect of first summer precipitation with a second-order term, the relationship was highly significant ($F_{1,420} = 12.07$, $P < 0.001$), while the linear term did not explain a significant amount of variance when added to this model ($F_{1,419} = 0.14$, $P = 0.707$). Change in wing patch size was highest after summers with intermediate amounts of precipitation, while it was lower after very dry or very rainy years (Fig. 1c). Change in forehead patch size was negatively related to the second winter NAO ($F_{1,473} = 7.72$, $P = 0.006$) (Fig. 1e), but unrelated to the first winter NAO ($F_{1,472} = 0.54$, $P = 0.462$), irrespective of age (age and interactions: $P > 0.655$).

Absolute ornament sizes

Wing patch size showed overall positive responses to the previous summer NAO ($F_{1,696} = 28.12$, $P < 0.001$) (Fig. 1b) and previous summer precipitation ($F_{1,674} = 13.39$, $P < 0.001$), but no response to previous winter NAO ($F_{1,695} = 2.32$, $P = 0.128$) or previous summer temperature ($F_{1,856} = 0.85$, $P = 0.357$). However, temperature showed a significant interaction with binary age ($F_{1,1085} = 8.87$, $P = 0.003$; age and other interactions: $P > 0.193$). Separate analyses for the two age classes revealed a strong negative relationship between previous summer temperature and wing patch size in yearlings ($F_{1,361} = 11.05$, $P = 0.001$), but a much weaker relationship in adults ($F_{1,395} = 4.60$, $P = 0.033$). When looking for non-linear effects of precipitation as predicted by the within-individual model, both the linear and the second-order terms explained a significant proportion of variance in wing patch size (linear: $F_{1,1036} = 9.25$, $P = 0.002$; second-order: $F_{1,1069} = 7.23$, $P = 0.007$) (Fig. 1d). Forehead patch size showed a strong negative response to the previous winter NAO ($F_{1,1025} = 8.30$, $P = 0.004$), but a much weaker relationship with current winter NAO ($F_{1,1576} = 3.94$, $P = 0.047$) (Fig. 1f), irrespective of binary age (age $F_{1,1311} = 21.79$, $P < 0.001$; interactions: $P > 0.413$).

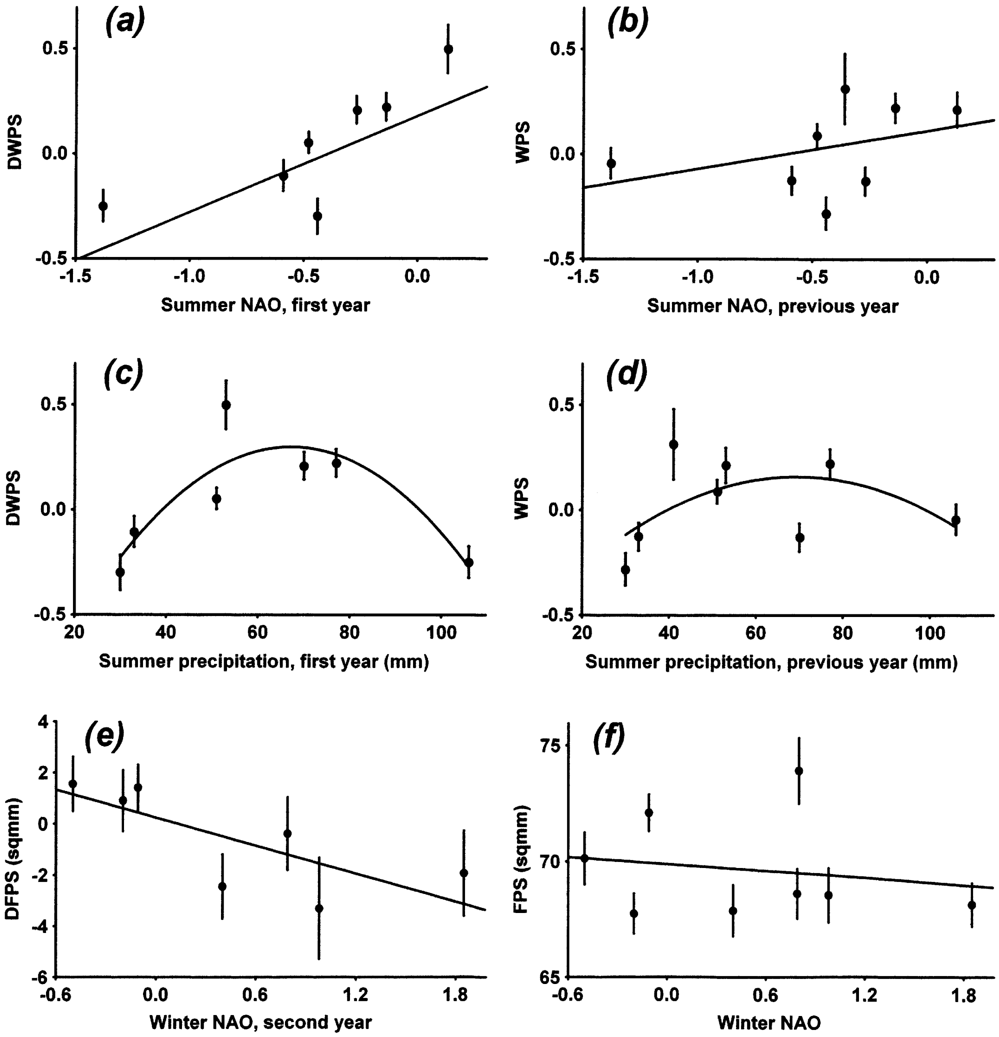

Fig. 1. Changes (a, c, e) and absolute sizes (b, d, f) of wing patch size (WPS) and forehead patch size (FPS) in relation to climate during moult (means ± standard errors). Change in ornament size (DWPS, DFPS) is expressed as a residual from a regression of ornament size on previous ornament size. The displayed values of wing patch size WPS and DWPS have been standardized for binary age.

Relative ornament sizes and sexual selection

The relative expression of forehead versus wing patches showed significant variation among years (year × ornament interaction: $F_{7,2074} = 4.10$, $P < 0.001$) (Fig. 2). After controlling for sexual selection on the other trait in a multiple regression (see Methods), breeding date selection on a given ornament in a particular year was negatively related to the relative expression of the trait in that year, although the relationship was only marginal for forehead patch size (wing patch size: $\beta = -0.48 \pm 0.17$, $t_5 = -2.89$, $P = 0.034$; forehead patch size: $\beta = -0.50 \pm 0.24$, $t_5 = -2.06$, $P = 0.095$) (Fig. 3). Stronger mate choice on a trait leads to an

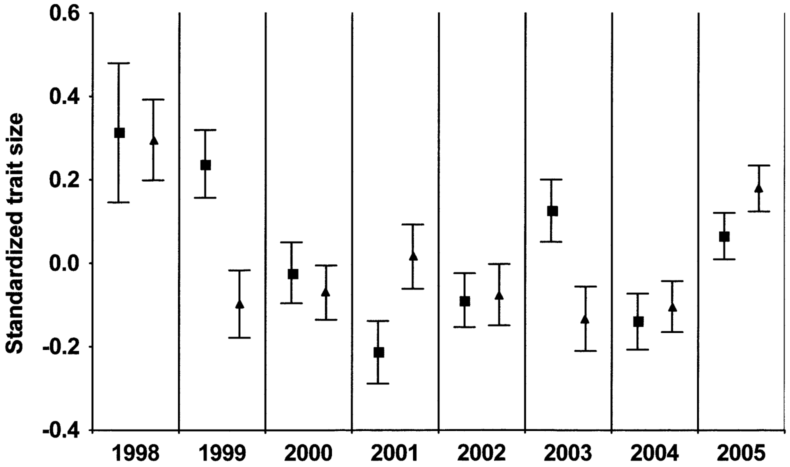

Fig. 2. Changes in the relative expression of two white plumage ornaments among years (means ± standard errors). Values refer to deviations from the overall mean of age-standardized trait size across the 8 years. ■, wing patch; ▲, forehead patch.

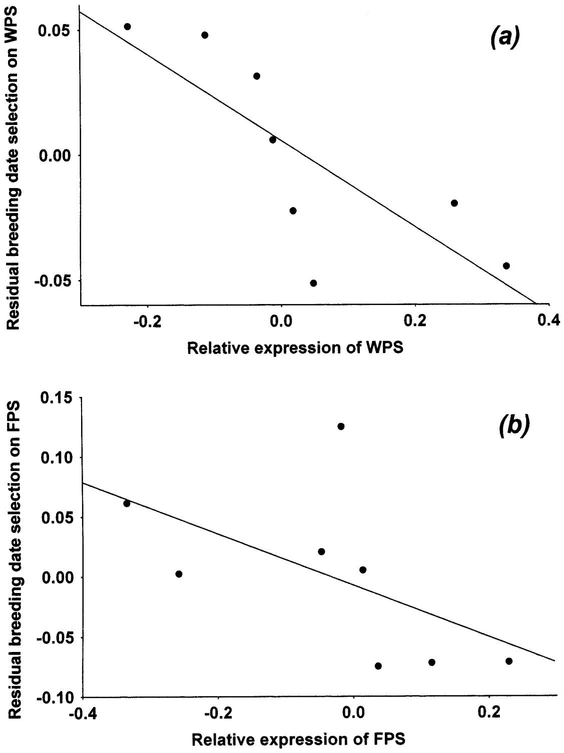

Fig. 3. Residual sexual selection gradients in terms of breeding date, in relation to the relative yearly expression of (a) wing patch size (WPS) and (b) forehead patch size (FPS).

increasingly negative relationship with breeding date. Therefore, our results suggest that sexual selection on a focal trait increased with the relative expression of the trait in a given year.

DISCUSSION

In this study, we assessed the sensitivity of two sexual signals to climatic conditions, considering environmental effects during the separate developmental periods of both signals, as well as the potential indirect effects of previous winter climate. Our results suggest that differential climatic effects on within-individual changes in trait sizes may translate to yearly fluctuations in relative trait sizes at the population level, and also illustrate how these fluctuations may affect patterns of selection. Finally, our results indicate multiple differences in sexual trait information content between two very closely related populations.

Climatic effects on patterns of sexual trait expression

The present analyses revealed different environmental influences on the two white plumage ornaments we examined. For example, we found an indirect winter climatic effect on changes in wing patch size. This effect is probably explained by a relationship between winter NAO and spring and early summer conditions at the breeding grounds (Przybylo *et al.*, 2000; Møller, 2002), which alter costs of reproduction (Gustafsson and Sutherland, 1988; Török *et al.*, 2004), and thereby influence sexual ornamentation (Gustafsson *et al.*, 1995). The indirect winter NAO effect on change in wing patch size was present only in yearlings, presumably due to their late breeding (Hegyi *et al.*, 2006) and the associated poor environmental quality (Török *et al.*, 2004) and larger moult–breeding overlap (our unpublished data). In contrast, changes in forehead patch size showed no indirect effect of the previous winter NAO, although costs of reproduction have been shown to influence the expression of forehead, but not wing patches in the Swedish population (Gustafsson *et al.*, 1995; Sheldon and Ellegren, 1999).

The expression of a plumage signal is most likely to correlate with the environmental conditions during its moult. There was a significant negative relationship between changes in forehead patch size and NAO at the winter moult, which was also mirrored by the population-level expression of the patch. The presence of this relationship is not surprising, given that patterns of precipitation and vegetation productivity at the sub-Saharan wintering range are predicted by the winter NAO (McHugh and Rogers, 2001; Oba *et al.*, 2001). However, Garant *et al.* (2004) showed a significant positive correlation between winter NAO values and the subsequent expression of forehead patch size in a Swedish population of our study species. The opposite signs of the effect in the two populations are in line with a previous study of population dynamics, which showed variation in the sign of NAO effects among relatively nearby populations (Sæther *et al.*, 2003). Changes and absolute values of wing patch size were predicted by precipitation at the breeding site during the summer moult in a bell-shaped manner, which suggests that both drought and excessive rains are harmful to the populations of insect food (DeGaetano, 2005). The spring and summer NAO have been found to correlate with patterns of precipitation (Zveryaev, 2004) and plant phenology in Europe (Lindholm *et al.*, 2001; Menzel, 2003), as well as the reproductive success of insectivorous birds in North America (Nott *et al.*, 2002). We found a positive effect of the summer NAO in addition to that of local weather on the changes in wing patch size of our birds. This may be due to flycatchers leaving the breeding site during or even before summer moult, after which they are no longer influenced by weather at this site. The impacts of precipitation and summer NAO on within-individual changes in wing patch size were clearly visible at the population level.

We also observed climatic effects on absolute ornament sizes that were not the consequence of within-individual changes. There was a negative effect of temperature in the year of birth on the wing patch size of yearlings. This may reflect either an age-specific environmental influence on the post-fledging moult of the ornament, or the interaction of summer temperature and wing patch size in determining the mortality or movements of first-year birds. Irrespective of age, absolute forehead patch size was negatively related to NAO in the preceding winter. Although differential movement of males cannot be ruled out as an explanation of this pattern, the indirect effect of winter climate on environmental suitability in the breeding season could interact with forehead patch size in determining the survival chances of males, which in turn affects the trait size distribution in the following year.

Climatic effects on sexual selection in multiple signal systems

Differential effects of large-scale environmental factors on multiple sexual signals may lead to shifts in the relative expression of multiple ornaments among years and habitat patches. We have shown that differences in both phenotypic plasticity and sensitive periods of two ornaments lead to contrasting relationships between ornament expression and environmental conditions in the two traits. These differential environmental effects may at least partly explain the significant fluctuation in the relative size of ornaments from one year to the next. Spatial fluctuations in trait size are also possible, given that part of the environmental predictors we identified are local.

Both forehead and wing patches are under directional sexual selection (Michl *et al.*, 2002; Garamszegi *et al.*, 2006; Hegyi *et al.*, 2006; our unpublished data). Collared flycatcher females probably either have innate preference functions (Forstmeier and Birkhead, 2004) or simply choose the more exaggerated traits due to an ‘arms race’ with signallers (Holland and Rice, 1998) or sensory bias (Endler *et al.*, 2001). Similar considerations can be applied to male competition. If receiver responses in either mate choice or male competition are open-ended, an increase in the population-level expression of a signal relative to other signals may also imply that generally more attention will be paid to this signal, which may lead to relatively stronger sexual selection on this trait. Therefore, a temporal pattern in the yearly relative expression of multiple ornaments may lead to shifts in the strength of sexual selection on these traits. Here we used breeding dates to test this idea. We found that sexual selection on wing patch size increased with an increase of the yearly mean expression of the signal relative to forehead patch size, and vice versa.

These results have several important implications. For example, environmentally mediated fluctuations in sexual selection may contribute to the maintenance of the additive genetic variability of sexual signals (Sasaki and Ellner, 1997; Day, 2000). Such patterns may also select for individual advertisement strategies whereby any male may choose to emphasize the more highly developed display trait (Johnstone, 1996), and individuals with poor ‘attractiveness genes’ may improve their mating chances or competition success by choosing an appropriate habitat for breeding and moult. The environment-dependent heritability of ‘good genes’ signals (Qvarnström, 1999; David *et al.*, 2000) could cause climatic effects on the relative information content of different ornamental traits. More importantly, however, our results suggest that differential macroclimatic effects on sexual signals may play a major role in shaping multiple signalling systems at the population level.

Condition-dependent sexual traits in migratory species generally respond to climate experienced at various stages of the yearly cycle (Garant *et al.*, 2004; Saino *et al.*, 2004a). Thus, the wide range of the ecological effects of anthropogenic climate change (Stenseth *et al.*, 2002) may also include the disruption of sexual selection processes. For example, if environmental conditions progressively deteriorate at the breeding grounds, but not at the wintering grounds (see, for example, Inouye *et al.*, 2000), this change will mainly affect the plumage ornaments that are developed in summer, but it will have less impact on ornaments grown in winter. Differential trait expression, in turn, may bias sexual selection towards the signal unaffected by the environmental change. This could lead to a further, evolutionary reduction of the costly, environmentally suppressed trait and, finally, to the collapse of the labile multiple signalling system (Pomiankowski and Iwasa, 1998). The effects of environmental variability limited to certain ornaments, areas, time periods, and ages could therefore represent an interesting extension of the 'match–mismatch' concept of climate change (Stenseth and Mysterud, 2002).

Signal information content

The reliability of sexual signals as indicators of individual quality is thought to be important to their sustained use as mate choice cues, because mate choice is accompanied by time, energy, and opportunity costs (Andersson, 1994; Pomiankowski and Møller, 1995; Cotton *et al.*, 2004; Tomkins *et al.*, 2004). Multiple signals used in mate choice may reflect different aspects of individual quality (Birkhead *et al.*, 1998; Doucet and Montgomerie, 2003), or provide the same information but reduce sampling costs (Backwell and Passmore, 1996) or amplify one another (Prum, 1990). There have been a number of studies on multiple ornamentation (e.g. Møller *et al.*, 1998; McGraw and Hill, 2000), but few of these have considered two or more ornaments of similar origin, although such comparisons could be important to determine if such traits also convey a similar message to the receivers (Lindström and Lundström, 2000).

Previous studies of up to 16 years, using body condition at fledging or in the breeding season, failed to detect condition-dependence in forehead patch size (Hegyi *et al.*, 2002, 2006), but did find a significant relationship for wing patch size (Török *et al.*, 2003). In the present study, wing patch size reflected multiple direct and indirect environmental effects, while forehead patch size was related only to climate directly at the winter moult. Moreover, the only climatic effect on the absolute patch sizes of adult birds unexplained by within-individual changes was the relationship of forehead patch size with NAO in the preceding winter. This effect may reflect climate-dependence in the mortality costs previously demonstrated for forehead patch size (Hegyi *et al.*, 2006) that are absent in wing patch size (Török *et al.*, 2003). Mortality costs of ornamentation are less likely in more condition-dependent traits (Rowe and Houle, 1996; Jennions *et al.*, 2001). We therefore conclude that forehead patch size has a smaller phenotypic plasticity in our population than wing patch size, in contrast to the Swedish population (Gustafsson *et al.*, 1995; Sheldon and Ellegren, 1999). The present results suggest multiple differences in the information conveyed by white patches between populations of a relatively recent common origin (Sætre *et al.*, 2001). This contributes to the accumulating evidence that the proximate determination of sexual signals evolves rapidly (Hegyi *et al.*, 2006; see also Griffith *et al.*, 1999; Badyaev *et al.*, 2001; Forstmeier and Leisler, 2004; Safran and McGraw, 2004). In summary, our results indicate that differential, year-specific environmental effects on different traits may have evolutionary implications, and should represent an important dimension in future studies on the information content and use of multiple sexual signals (Candolin, 2003).

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