

Rapid temporal change in the expression and age-related information content of a sexually selected trait

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Abstract

The expression of sexual signals is often phenotypically plastic and also evolves rapidly. Few studies have considered the possibility that proximate determination – the pathway between genes and trait expression – may also be subject to both phenotypic plasticity and evolutionary change. We examined long-term patterns in size, condition- and age-dependence, repeatability and heritability of forehead patch size, a sexually selected plumage trait in male collared flycatchers. We also estimated survival and sexual selection on the phenotypic value of the trait. Forehead patch size linearly declined during the 15 years, probably due to the significantly negative survival selection. In addition, the expression of genetic variation for the ornament apparently underwent an age-limited change, which implies a change in the information content of the signal to receivers. The persistent lack of condition-dependence makes phenotypic plasticity an unlikely explanation to our results. This raises the possibility of a microevolutionary change of both expression and proximate determination during the study period.

Introduction

The adaptive value of elaborate traits and the costs and benefits of using them for choice of a mate or settling a conflict have been a central topic of evolutionary ecology (Andersson, 1994; Andersson & Iwasa, 1996). Less attention has been paid to the evolutionary dynamics of these signals, including changes in their expression and information content. Comparative studies repeatedly suggested that sexually selected traits are labile characters with high levels of homoplasy, so they are not suitable for clarifying phylogenetic relationships (Price & Birch, 1996; Kusmierski *et al.*, 1997; Omland, 1997; Prum, 1997; Wiens, 1999; Omland & Lanyon, 2000). There is abundant evidence for variation of sexual signals among populations of a single species (Røskaft & Järvi, 1992; Hill, 1994; Young *et al.*, 1994; Camplani *et al.*, 1999; Ödeen & Björklund, 2003; Soha *et al.*, 2004), which is also suggestive of rapid evolution of these characters.

The benefits of mate choice based on the expression of a given character are seriously affected by the message encoded in the trait. This message is determined in part

by the extent to which physiological and nutritional state influences the expression of the signal, that is, condition-dependence (Ligon *et al.*, 1990; Evans, 1991; Norris, 1993; Thompson *et al.*, 1997; McGraw *et al.*, 2002; Badyaev & Duckworth, 2003). Genetic determination of signals may constitute another benefit to the choosy sex, through the attractiveness and future mating success of offspring (Pomiankowski & Møller, 1995; Roulin *et al.*, 1998). Finally, genetically determined attributes that exert a long-term influence on the body condition of an individual may form the basis of 'good genes' signalling, which is an interface between condition-dependence and genetic determination (Rowe & Houle, 1996; Saino *et al.*, 1997; Qvarnström, 1999; Johnsen *et al.*, 2003; Török *et al.*, 2003). In sum, the information content of a signal is determined by the combination of condition-dependence, genetic background, and their interaction.

Variation in the information content of a signal between populations is not a widely recognized phenomenon. Genetically based differences may result, for example, from depletion of additive genetic variance for a trait in one population but not in others, as suggested for forehead patch size in a population of pied flycatchers (Dale *et al.*, 1999). In contrast, divergence of the degree of condition-dependence with similar genetic variability has been found in collared flycatchers *Ficedula albicollis* (Hegyí *et al.*, 2002). Environmentally based population

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differences in signal information content are also possible. In an island population of house sparrows *Passer domesticus*, the supplementation of nestboxes apparently altered the importance of individual attributes to breeding success. This, in turn, may have led to the observed reversal of sexual selection on the black bib size of males (Griffith *et al.*, 1999a). Shifts in relationships among components of carotenoid ornamentation between two house finch (*Carpodacus mexicanus*) populations have been explained by parasite-mediated difference in carotenoid limitation (Badyaev *et al.*, 2001).

Some of the above mentioned studies suggest that the widely documented evolutionary flexibility of ornamental traits (Wiens, 2001) may extend to their genetically determined information content. These studies, however, did not provide information on the timescale, direction, or adaptive value of evolutionary shifts in information content, which have so far been discussed only in theoretical studies (Rowe & Houle, 1996; Kokko *et al.*, 2002). On the other hand, different expression of genetic variance in different environments has been widely documented for morphological and physiological traits, including some studies on sexual signals (Tomkins *et al.*, 2004). Moreover, a recent study on house finches raised the possibility that the allocation of resources to sexual ornamentation may itself show adaptive plasticity. Unmated males invested more into ornamentation than mated males, and condition-dependence of ornamentation declined with age (Badyaev & Duckworth, 2003). In the context of long-term studies, analysing condition-dependence may represent a way to distinguish between genetic vs. environmental changes, or in other words, microevolution vs. phenotypic plasticity of information content. At present, however, data on changes of even the expression of sexually selected traits within natural populations are scarce (Coltman *et al.*, 2003; Garant *et al.*, 2004; Møller & Szép, 2005). No study looked for systematic temporal patterns in the messages encoded in, or conveyed by, these traits. Here we present detailed analyses of a sexually selected plumage trait in a long-term dataset of individually marked individuals and their offspring to reveal any shifts in expression or proximate determination of the signal with time.

The collared flycatcher is a small, long-distance migratory, sexually dichromatic, hole-nesting passerine. Due to the high between-year site fidelity of adults it is possible to follow individuals throughout their life. This attribute makes the species a suitable object of studies ranging from life history (Gustafsson & Sutherland, 1988) to morphological evolution (Merilä *et al.*, 2001). The white forehead patch of males is grown during the partial moult at the winter quarters in South Africa (Cramp & Perrins, 1993). The proximate determination of this ornament has been studied in detail in two populations on the Swedish island of Gotland and in Pilis Mountains, Hungary. Forehead patch size is sexually selected in both populations (Qvarnström *et al.*, 2000;

Michl *et al.*, 2002). The heritability and repeatability of the trait is high at both sites, but the degree of phenotypic plasticity differs. In the Swedish population, forehead patch size was related to age and body condition during the previous breeding season (Gustafsson *et al.*, 1995; Qvarnström, 1999), and reflected yearly fluctuations in climatic conditions (Garant *et al.*, 2004). In the Central-European population, in contrast, dependence of the trait on age, body condition, yearly food supply and climatic variables was weak (Hegyi *et al.*, 2002, our unpublished data). We use a 15 year dataset to look for temporal shifts in size, condition-dependence, age-dependence and genetic background of forehead patches in the Hungarian population. To see the extent to which the temporal patterns of expression and information content are consistent with natural or sexual selection, we also examine if survival or breeding date is related to forehead patch size, and if the relationship changed with time. As not only the expression, but also the role and information content of sexual signals have been shown to depend on age (Grahn & von Schantz, 1994; Badyaev & Duckworth, 2003), we perform the analyses of proximate determination and selection in two age categories (yearling and older males). We use tarsus length as a 'control' trait to see if changes in the expression and heritability of general morphology explain our results.

Materials and methods

Field methods

Collared flycatchers have been continuously studied in Pilis Mountains, Hungary, from 1982. Our plots cover parts of a continuous oak woodland where a total of about 800 nestboxes were placed in a grid system. The density of nestboxes is within the range of natural nest site densities reported for unmanaged forests (van Balen *et al.*, 1982), which is in turn much higher than the availability of natural holes in the managed forests surrounding the study site. Breeding site fidelity of returning individuals is very high (Hegyi *et al.*, 2002). Approximately 20–40% of nests produce breeding recruits in the long term (Török *et al.*, 2004).

Males were caught at various times from their arrival onwards, but most of them while feeding endothermic nestlings. Forehead patch size was estimated as the product of maximum height and maximum width taken with a dial caliper to the nearest 0.1 mm. Recent studies suggested that width and height may function as separate ornaments with different information content (Griffith & Sheldon, 2001; Kilpimaa *et al.*, 2004). However, conducting the tests separately for the two dimensions did not yield qualitative difference in any of the cases, so we report results for area throughout. Repeatabilities of the measurers involved were not significantly different (as estimated in an ANCOVA from between-season datapairs

on the same birds), and systematic differences among them were corrected for based on mean forehead patch values taken in the same seasons. A dataset limited to the two most experienced persons (approx 60% of data) yielded results virtually identical to those presented here. Tarsus length of males was measured with a caliper to the nearest 0.1 mm. Start of breeding (day of the first egg) was known from frequent checks of the plots during the nesting period. Data come from the 15 field seasons of 1990–2004.

Statistical analyses

To avoid pseudoreplication, we used the first measurement, or the first pair of measurements from each male in horizontal and vertical tests, respectively. With the number of nestlings recaptured, it was not possible to safely interpret correlations for heritabilities and recruit condition-dependence on a yearly basis. We therefore divided the study period into two equal time intervals (date of birth 1990–1996 and 1997–2003), and compared these in general linear models. However, to detect potential artefacts due to the period coding, we also conducted a tentative heritability analysis with year as a covariate.

Collared flycatchers rarely live longer than 3 years, although a few individuals older than 5 years are encountered each year. Time- and age-dependence of forehead patch size was therefore analysed in a two-way ANOVA with year and three age categories (second-year, third-year and older) as factors. To assess within-individual changes of the trait we used three age transition classes (after second year, after third year and older) as a factor, year as a covariate, and within-individual change as a repeated measures factor. As little age-dependence was detected in either the horizontal or the within-individual analyses, we used a binary age classification in the subsequent tests (yearling or older). Since yearlings wear a subadult plumage (Cramp & Perrins, 1993), it is reasonable to expect differences in the proximate determination and role of ornamentation between these age classes.

To see whether forehead patch size is adjusted to individual state, we assessed the relationship between the ornament size of recruits and their body condition at fledging (body mass-tarsus length residuals; Qvarnström, 1999). Fledgling body condition reflects food supply during development (Török *et al.*, 2004), and it is under linear survival selection (Lindén *et al.*, 1992; our unpublished data). Early condition-dependence was assessed on the heritability dataset described below. Our model included father and offspring binary age and period as factors, paternal badge size and year- and paternal age-standardized fledgling condition as covariates, and son badge size as a dependent variable. To facilitate population comparison, we also calculated the model of Qvarnström (1999): a multiple regression with father

badge size and fledgling condition as covariates, and son badge size as dependent variable.

Repeatability was calculated by using binary age as a factor, year and actual badge size as covariates, and next-year badge size as dependent variable. For the heritability analyses, we averaged all recruits from the same father, irrespective of their nest of origin (i.e. primary or secondary). If a male recruited offspring from more than one season, only the first year was used here, because we aimed to characterize temporal changes in heritabilities. Although few recruits came from nests of subadult males, all fathers were considered in the heritability analyses. Heritability was assessed with period and the ages of son and father as factors, father badge size as a covariate, and son (or son-average) badge size as a dependent variable. To ensure that the arbitrary selection of time intervals did not bias our results, we also run a model which included year as a covariate instead of periods. The heritabilities we report here are probably influenced by extra-pair paternity in relation to age and forehead patch size (Michl *et al.*, 2002, also see section 'Discussion').

To see if any age-dependence in expression and information content of forehead patch size can be linked to trait-related survival patterns, we analysed the return rate of males in two age classes. The forehead patch size of subadults only influences survival to the next breeding season, when they grow their adult patch. Thus, to obtain estimates which are comparable between the two ages, we estimated survival as recapture of the individual in the subsequent breeding season. This method does not take recapture probability into account (Møller & Szép, 2005). However, a mark-recapture analysis confirmed our present results for adult males (our unpublished data). For the present purpose, survival was analysed in a generalized linear model with binomial error and logit link, recapture as the dependent variable, binary age as a factor and year as well as year-standardized forehead patch size as covariates. In males which were caught both as subadults and as adults, the subadult datum was used. In addition, yearly survival selection differentials were calculated by regressing relative survival (0 = died, 1 = survived, divided by the yearly mean) on standardized forehead patch size (Arnold & Wade, 1984).

In the absence of data on extrapair paternity (Sheldon & Ellegren, 1999), we use breeding date (first egg date) to estimate sexual selection on forehead patch size. We rarely recorded the arrival date of males to the area. However, as forehead patch size is unrelated to body condition (Hegyi *et al.*, 2002; this study), its relationship with breeding date is unlikely to reflect arrival date and probably results from male competition, female choice, or both. Because of the skewed distribution of breeding dates, we used a binary measure (1, before or at the yearly median; 2, after the yearly median). Data were analysed in a generalized linear model similar to that used for survival data (see above). Yearly breeding date selection differentials were calculated by regressing

relative breeding date (0 = early, 1 = late, divided by the yearly mean) on standardized forehead patch size (Arnold & Wade, 1984).

To see if selection on, or patterns of body size explained changes in forehead patch size or its information content, the horizontal, heritability, survival and breeding date analyses described above were repeated for tarsus length. We also entered individual tarsus length as a covariate into the horizontal and the selection analyses of forehead patch size. All statistical tests are two-tailed and were calculated in Statistica 5.5. Means are reported with their standard errors. We applied backward model selection to increase power in the analyses of heritability, condition-dependence and selection. We removed nonsignificant interactions and independent variables (unless with a significant interaction), starting with the highest-order, least significant interactions. The removed terms were then re-entered to the final model one by one.

Results

Temporal trend and within-year correlates

Forehead patch size strongly varied among years ($F_{14,1454} = 4.155$, $P < 0.001$), but not among age categories ($F_{2,1454} = 2.282$, n.s.; year \times age $F_{28,1454} = 0.793$, n.s.). The temporal change proved to be a linear decline (Fig. 1, ANCOVA with age as a factor and year as a covariate; year: $F_{1,1495} = 77.135$, $P < 0.001$). Forehead patch size tended to level off in the final years of the study (second-order polynomial regression; $F_{1,1497} = 121.022$, $P < 0.001$), but the polynomial term did not explain a significant amount of residual variance when the linear decline was controlled for ($F_{1,1496} = 2.189$, n.s.). Tarsus length also declined during the study period (ANCOVA, $F_{1,1471} = 24.657$, $P < 0.001$), but entering tarsus length as a second covariate into the analysis of forehead patch size only very slightly reduced the effect of time on the ornament (ANCOVA, $F_{1,1468} = 71.992$, $P < 0.001$).

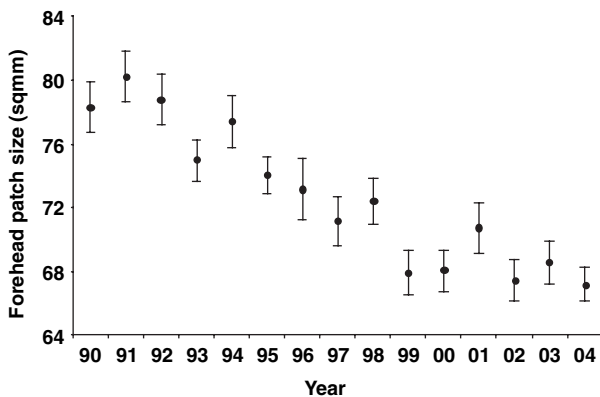


Fig. 1 Yearly means (\pm SE) of forehead patch sizes, male age classes pooled.

Within-individual changes

Forehead patch size showed little change with age overall (repeated measures ANCOVA; year $F_{1,426} = 33.947$, $P < 0.001$; age class $F_{2,426} = 0.730$, n.s.; repeated measure $F_{1,426} = 0.734$, n.s.). None of the interactions were significant ($P > 0.08$). Repeatability of forehead patch size was high (ANCOVA; previous badge $F_{1,429} = 295.030$, $P < 0.001$) and did not change with time, age or their interaction ($P > 0.41$). The overall between-year repeatability (year-standardized values) was $R = 0.650 \pm 0.037$.

Heritability and early condition-dependence

The overall heritability estimate of forehead patch size was 0.345 ± 0.116 . However, heritabilities were significantly related to the interaction between recruit binary age and period (Table 1, Fig. 2). They were similar for subadult and adult recruits in the first period ($F_{1,104} = 0.382$, n.s.), but reversed in sign among subadults ($F_{1,102} = 5.237$, $P < 0.05$) and did not change in adults ($F_{1,115} = 1.723$, n.s.), which lead to a significant difference between the two age categories in the second period ($F_{1,115} = 9.020$, $P < 0.01$). The interaction between period and recruit age on recruit ornament size itself was also significant. The forehead patch size of subadult recruits decreased with time relative to that of their father ($F_{1,102} = 3.383$, $P = 0.068$), while there was no such change in adult recruits ($F_{1,118} = 0.360$, n.s.).

Binary age of the father and all of its interactions were nonsignificant, but this may be due to the small number of recruits from subadult fathers. The heritability estimates (reported in Fig. 2) are similar and positive for all combinations of father and recruit ages in the first period. In the second period, however, all slopes except for adult fathers and adult recruits are negative or close to zero. When we pooled father-son pairs with a subadult father, a subadult son or both and compared them to the pairs with adult fathers and adult sons, there was a significant time \times group effect on heritability (time \times group \times badge of father $F_{1,219} = 9.622$, $P < 0.01$), with the forehead patch similarity significantly decreasing in the first group ($F_{1,120} = 4.943$, $P < 0.05$), but not changing in the second group (see above).

Conducting the heritability tests with year as a covariate revealed similar patterns, with a significant effect of paternal badge size ($F_{1,219} = 5.638$, $P < 0.05$), and significant interactions between year and recruit age ($F_{1,219} = 4.858$, $P < 0.05$) and between year, recruit age and paternal badge size ($F_{1,219} = 8.494$, $P < 0.01$). The changes in heritabilities with continuous time were nonsignificant in both age categories, but the tendency was negative in subadult recruits ($F_{1,102} = 2.075$, $P = 0.153$) and positive in adult recruits ($F_{1,115} = 2.852$, $P = 0.094$). We note that the median yearly sample size per age category was $n = 9$ (range 2–22), so the power of the

	Forehead patch	Tarsus length	Forehead patch and body condition
Period	3.236 (1,219)	4.551 (1,214)	0.848 (1,165)
Recruit age	5.920* (1,219)	6.928** (1,214)	0.759 (1,165)
Father age	0.017 (1,218)	1.811 (1,213)	0.104 (1,165)
Condition			1.336 (1,164)
Trait size of father	5.263* (1,219)	4.979* (1,214)	5.442* (1,165)
Period × recruit age	6.805** (1,219)	0.003 (1,213)	7.986** (1,165)
Period × father age	0.401 (1,217)	1.566 (1,212)	0.417 (1,164)
Recruit age × father age	0.027 (1,217)	1.902 (1,212)	14.802*** (1,165)
Period × condition			3.313 (1,163)
Recruit age × condition			0.382 (1,163)
Father age × condition			2.856 (1,163)
Period × trait size of father	0.391 (1,218)	0.020 (1,213)	0.082 (1,164)
Recruit age × trait size of father	2.772 (1,218)	3.472 (1,213)	0.625 (1,164)
Father age × trait size of father	0.219 (1,217)	0.028 (1,212)	0.517 (1,164)
Condition × trait size of father			0.195 (1,163)
Period × recruit age × father age	0.189 (1,217)	0.747 (1,212)	0.402 (1,164)
Period × recruit age × condition			2.262 (1,163)
Period × father age × condition			0.801 (1,163)
Recruit age × father age × condition			0.364 (1,163)
Period × recruit age × trait size of father	7.562** (1,219)	0.003 (1,213)	10.137** (1,165)
Period × father age × trait size of father	0.436 (1,217)	1.566 (1,212)	0.804 (1,164)
Recruit age × father age × trait size of father	0.178 (1,217)	2.061 (1,212)	18.410*** (1,165)
Period × condition × trait size of father			2.649 (1,163)
Recruit age × condition × trait size of father			0.348 (1,163)
Father age × condition × trait size of father			2.249 (1,163)

Displayed are *F* values with effect and error degrees of freedom in parentheses. Error degrees of freedom vary within tests due to the step-wise backward model selection.

**P* < 0.05.

***P* < 0.01.

****P* < 0.001.

latter analysis to detect age-restricted heritability changes is very low. In conclusion, the father-offspring similarity in forehead patch size apparently declined with time for both subadult fathers and subadult offspring and only the combination of adult fathers and adult sons remained unaffected by this change. The heritability of tarsus length, in contrast, showed no significant relationship with either age or time (Table 1).

When we entered body condition at fledging into the model of forehead patch size heritability, neither its main effect, nor any of its interactions were significant (Table 1). For comparability with the Swedish population, we also performed a multiple regression with unstandardized condition at fledging and father badge size as independent variables and son badge size as dependent variable. The effect of condition was negative and very far from significance ($\beta = -0.037 \pm 0.075$, $t_{171} = -0.490$, n.s.).

Selection on forehead patch size

Survival of males ($n = 446$ subadults and $n = 907$ adults) was significantly affected by forehead patch size ($Wald = 4.275$, $P < 0.05$) and the interaction between year and forehead patch size ($Wald = 4.302$, $P < 0.05$).

Table 1 Changes in the expression of genetic variation for tarsus length and forehead patch size, and in the early condition-dependence of forehead patch size; general linear models.

The effect of time, age and all other interactions were nonsignificant ($Wald < 0.691$). Survivors had smaller forehead patches than nonsurvivors in ten of the 14 years, and the intensity of selection increased with time (Fig. 3a). Tarsus length was also marginally negatively related to survival (not shown), but in a model with both tarsus length and badge size as covariates, only the increasing effect of forehead patch size was significant (tarsus length $Wald = 2.239$, n.s.; forehead patch size $Wald = 4.384$, $P < 0.05$; year* forehead patch size $Wald = 4.412$, $P < 0.05$; all other terms $Wald < 0.901$, n.s.).

Breeding date of males was most strongly affected by binary age, with subadult males breeding much later than adults ($Wald = 103.851$, $P < 0.001$). In addition, breeding date was also related to year ($Wald = 15.777$, $P < 0.001$) and forehead patch size ($Wald = 8.024$, $P < 0.01$). The year effect was probably due to differences in the distribution of breeding date between years. All interactions were nonsignificant ($Wald < 0.861$, n.s.). Early breeding males had larger forehead patches than late breeders in 13 of the 15 years, and the intensity of selection did not change with time (Fig. 3b). Tarsus length alone also negatively correlated with breeding date (not shown), but in a model with

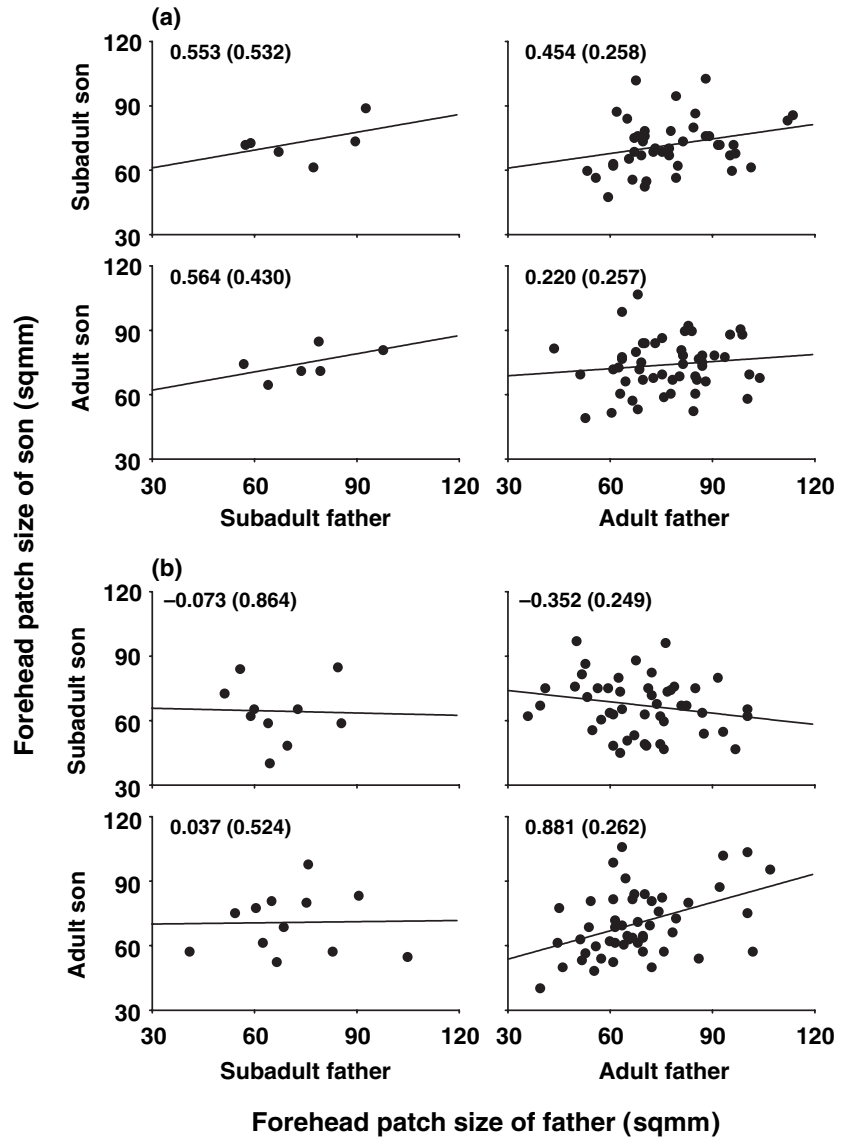


Fig. 2 Son average/father regressions of forehead patch size in relation to offspring and father age and time period of birth; (a) 1990–1996, (b) 1997–2003. The heritability estimates for the separate groups [twice the slopes (SE) of the lines] are reported.

both tarsus length and badge size as covariates, the effects of both traits were significant (year $Wald = 17.569$, $P < 0.001$; age $Wald = 104.668$, $P < 0.001$; tarsus length $Wald = 4.092$, $P < 0.05$; forehead patch size $Wald = 8.697$, $P < 0.01$; all interactions $Wald < 2.794$, n.s.).

Discussion

Change in signal expression

Laboratory studies of species with short generation times have repeatedly demonstrated that sexual signals readily react to selection, showing substantial changes within a few generations (Wilkinson, 1993), but there are very few long-term analyses from natural populations (Coltman *et al.*, 2003; Møller & Szép, 2005). As judged from

fertilization patterns, forehead patch size seems to be favoured by female-controlled extrapair paternity in our population (Michl *et al.*, 2002), which is a strong selective agent in this predominantly socially monogamous species (Sheldon & Ellegren, 1999). In addition, here we show that date of breeding is also significantly negatively related to forehead patch size (Fig. 3b). Breeding date may be one of the most important determinants of seasonal reproductive success in our population (Garamszegi *et al.*, 2004; Török *et al.*, 2004). In spite of the apparent sexual selection advantage, which increases reproductive success of large-patched males, forehead patch size showed a significant, linear decline with time (Fig. 1). There are several potential explanations to this pattern.

The change in the trait may reflect environmental change through phenotypic plasticity. However,

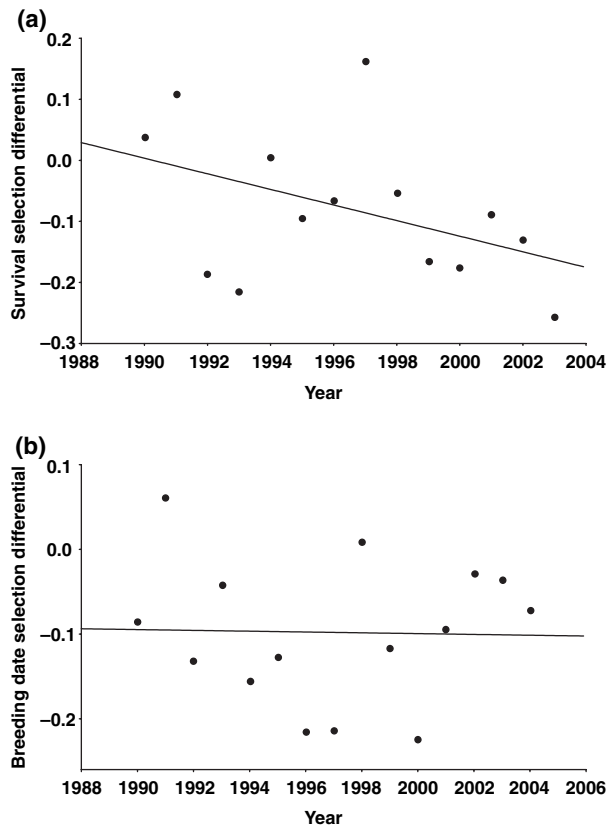


Fig. 3 The temporal pattern of selection differentials on forehead patch size by (a) survival to the following breeding season and (b) breeding date relative to the yearly median. Note that breeding date is negatively related to fitness.

within-individual changes of forehead patch size were not significant in any age category. Moreover, the plasticity of forehead patch size seems very small in our population, as judged from its condition-independence (also see section 'Change in signal information content'). Male survival declined with increasing forehead patch size irrespective of age category, and the relationship strengthened with time (Fig. 3a). A temporal change in the environment (e.g. forest succession, quality of the nestboxes, population density) could have led to non-random movements of males in relation to their forehead patch size between the study plots and nest sites in the surrounding woodlands, resulting in patch size change and apparent survival selection. A permanent emigration of large-patched males from the plots is unlikely because collared flycatchers show very high site fidelity between years (Hegyi *et al.*, 2002), and they prefer nestboxes to natural nest sites because of the higher breeding success achieved in the former (Gustafsson, 1988; Alatalo *et al.*, 1990).

Alternatively, the apparent decline in badge size may be a genetic response to directional selection. Response to

selection requires significant additive genetic background, which seemed to be present during the study period, although only experimental studies can rule out environmental effects on parent-offspring similarity (see section 'Change in signal information content'). The change in trait size was linear, with a tendency to level off in the last years of the study period. Although breeding date selection did not change and survival selection increased with time, the expression of genetic variance apparently declined in the subadult age class (see section 'Change in signal information content'), which may have reduced the potential of forehead patch size to respond to selection. Correlated response to selection on other traits cannot be ruled out as an alternative explanation to the patch size decline, but entering body size (tarsus length) as a covariate into the analyses did not change the results for forehead patch size in either the horizontal or the selection analyses. Thus, differential survival in relation to the trait itself probably contributed to the decrease of forehead patch size. Few studies have established a negative relationship between natural, nonmanipulated expression of a sexual signal and viability in birds and the overall pattern was positive (Jennions *et al.*, 2001). We note that although mating selection was positive and did not change significantly during the study period, different levels of sexual selection are not necessarily correlated (Delhey *et al.*, 2003), so we cannot rule out other influences of sexual selection on the patch size change via unmeasured fitness components such as cuckoldry or polygyny. As collared flycatchers wear a cryptic colouration without forehead patch during the winter months (Cramp & Perrins, 1993), the apparently poorer survival of large-patched males was probably due to costs at the breeding grounds, including male-male aggression in relation to the trait (Qvarnström, 1997) and predation on attractive and conspicuous individuals (Slagsvold *et al.*, 1995). These effects may have strengthened with the increase of breeding density at the establishment of our nestbox plots in 1982 (Török & Tóth, 1988).

Change in signal information content

Sexually selected traits may exhibit temporal changes not only in their level of expression, but also in the information they convey, in response to changing selection pressures. This may involve changes in condition-dependence (Rowe & Houle, 1996; Kokko *et al.*, 2002), or in the structure and expression of direct genetic determination (Beldade *et al.*, 2002). Although many authors reported apparent population differences in information content (e.g. Alatalo *et al.*, 1994; Dale *et al.*, 1999; Hegyi *et al.*, 2002), few long-term studies have examined the speed and direction of changes in the proximate determination of ornamental traits.

We found that forehead patch size was independent of body condition at fledging. Phenotypic plasticity is the

potential of individuals to adjust the expression of a given trait in response to environmental changes (Piersma & Drent, 2003). Perhaps the most important evolutionary advantage of the phenotypic plasticity of sexual signals is the possibility to reduce costs by adjusting signal expression to body condition (Rowe & Houle, 1996). In both the Swedish population of Gotland and our population, fledging condition is sensitive to rearing conditions and it is under strong positive survival selection (Gustafsson & Sutherland, 1988; Lindén *et al.*, 1992; Török *et al.*, 2004; our unpublished data). Qvarnström (1999) reported a positive relationship between body condition at fledging and badge size as a recruit in Gotland, but this relationship was negative and nonsignificant in our case. This difference is in line with our previous results for adult body condition, and suggests that the condition-dependence of the ornament, and the advantage of females from choosing large-patched males differ between the populations (Hegyi *et al.*, 2002). The condition-independence of forehead patch size in our birds persisted throughout the study period, in spite of the apparently high wearing costs of the trait. This is interesting in light of previous studies showing changes in the quality indicator value of ornaments in relation to age and social context (Grahn & von Schantz, 1994; Badyaev & Duckworth, 2003). The persistence of condition-independence also raises the question of how likely are genetic changes leading to the emergence of a condition-dependent variant in a population, which is likely to spread if it appeared (Rowe & Houle, 1996). The lack of opportunity for within-individual adjustment may also partly explain the steeper decline of forehead patch size in our population than in Sweden (see Garant *et al.*, 2004), but differences in patterns of selection cannot be ruled out. Within individuals, forehead patch size showed no significant age-dependence and this did not systematically change during the study period. This also contradicts the patterns observed in the Swedish population (Gustafsson *et al.*, 1995). In sum, the phenotypic flexibility of forehead patch size seems very low in our population.

Although static and opposing effects of sexual and viability selection would quickly deplete additive genetic variance, the additive genetic variability of sexual signals is generally higher than that of nonornamental traits (Pomiankowski & Møller, 1995). Our results seem consistent with these findings, as the overall heritability of forehead patch size did not decline over the 15 years. However, the details behind the similar overall heritability were very different early and late in the study period. In contrast to the inflexibility of condition-independence, the expression of genetic variation and consequently the information content of forehead patch size in the subadult age class seem to have qualitatively changed during the 15 years. There was a substantial drop of father-offspring similarity for both subadult fathers and subadult sons (Fig. 2). The heritability

estimate for adult fathers and adult offspring did not change significantly, and even tended to increase during the study period. In addition, the forehead patch size of subadult recruits became smaller relative to that of their father, while no such change was observed in adult recruits.

Temporal change in age-related extrapair paternity (e.g. Wetton *et al.*, 1995; Richardson & Burke, 1999) would be a straightforward explanation to this pattern, but the heritability of morphology (tarsus length) showed no significant variation with either age or time. Selection before recruitment due to increased territorial competition restricted to the subadult age class also cannot account for the pattern, as the variance of forehead patch size of subadult recruits did not decline during the study (Bartlett $\chi^2 = 0.495$, d.f. = 1, n.s.; see Fig. 2). Early environmental effects reducing the expression of genetic variance (Merilä, 1997; Qvarnström, 1999; Merilä *et al.*, 2001; Charmantier *et al.*, 2004; Garant *et al.*, 2004) or maternal effects through the egg in relation to paternal age and attractiveness (Gil *et al.*, 1999; Strasser & Schwabl, 2004) are unlikely to have caused the heritability changes, as the trait showed no effect of either early development or adult condition (Hegyi *et al.*, 2002; this study). This raises the possibility of a microevolutionary change in the expression of genetic variance during the study period, with males increasingly growing small badges as yearlings, and resembling their fathers only later in life. The adaptive value of this pattern may be to reduce the wearing costs of forehead patch size, e.g. the increasing survival disadvantage we detected, in a situation when reproductive success is low in any case, due to the late arrival of subadult males to the breeding grounds (Gustafsson, 1989). However, experiments are needed to control for environmental determinants of father-son similarity including maternal effects (Griffith *et al.*, 1999b; Forstmeier *et al.*, 2004), and to clarify the degree of condition-dependence (Tomkins *et al.*, 2004), so our purely correlative results are insufficient to rule out the alternative explanations.

In conclusion, we have demonstrated that the size of a plumage signal declined with time, in line with the directional survival selection against the trait. The patterns of father-offspring similarities suggest an age-related change in the expression of genetic variation for the ornament, with subadult males increasingly masking their genetically determined ornament size. Our results are therefore consistent with recent theory and empirical data suggesting that a mate-choice signal may not only be reduced in expression among subadults as compared to adults, but also its information content may differ between the age classes (Grahn & von Schantz, 1994; Proulx *et al.*, 2002; Badyaev & Duckworth, 2003). The apparent lack of phenotypic plasticity suggests that within-individual adjustment does not explain the observed changes in trait expression and information

content. Further, experimental studies are needed, however, to directly demonstrate evolutionary changes in the message conveyed by sexually selected traits (Rowe & Houle, 1996; Kokko *et al.*, 2002). The results of these will have broad implications from the models of signal-preference coevolution and multiple signalling (Møller & Pomiankowski, 1993; Schluter & Price, 1993; Holland & Rice, 1998; Pomiankowski & Iwasa, 1998) to the role of genetic quality signals in adaptation to the prevailing environment (von Schantz *et al.*, 1996; Hoekstra *et al.*, 2001; Coltman *et al.*, 2003; Lorch *et al.*, 2003).

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