

Qualitative population divergence in proximate determination of a sexually selected trait in the collared flycatcher

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Abstract

We examined proximate determination of sexually selected forehead patch size in a Central-European population of *Ficedula albicollis*, the collared flycatcher, using a 9-year database, and compared our results with those obtained in other populations of the same and the sister species. Between-individual variation of forehead patch size was large, its repeatability larger than, and heritability similar to the Swedish population. Unlike in the other populations, the trait proved unaffected by body condition, and only very slightly influenced by age. There was no relationship between forehead patch size and breeding lifespan, and a marginal negative association with survivorship in adult males. Our results suggest that additive genetic variance of the trait in this population is large, but genes act independently of body condition, and there is no viability indicator value of the trait. This is the first report of a qualitative intraspecific difference in proximate determination of a sexually selected trait.

Introduction

Female choice in relation to male secondary sex traits may confer various benefits to the limiting sex. One of them is genetic quality of the young (Petrie *et al.*, 1998), including viability (von Schantz *et al.*, 1989; Møller, 1994; Nicoletto, 1995; Freeman-Gallant, 1996; Hasselquist *et al.*, 1996) or attractiveness (Houde, 1992; Roulin *et al.*, 1998). Other alternative explanations are, for example, reduced risk of infection (Clayton, 1990; Spurrier *et al.*, 1991; Gustafsson *et al.*, 1994; Soler *et al.*, 1999), territory quality (Strain & Mumme, 1988; Radesäter & Jakobsson, 1989), and paternal contribution to offspring care (Nisbet, 1973; Palokangas *et al.*, 1994; Sætre *et al.*, 1995). Female preference may also be a result of selection pressures on the sensory system unlinked to reproduction (Enquist & Arak, 1994; John-

stone, 1994; Ryan, 1998). Females in some species use multiple cues to evaluate candidates (Zuk *et al.*, 1992; Beani & Dessì-Fulgheri, 1995; Collins & ten Cate, 1996; Dale & Slagsvold, 1996; Howard & Young, 1998; Hill *et al.*, 1999) and there may be difference between populations of a single species with respect to dominant choice criteria (Dale *et al.*, 1999) as well as preferred trait values (Freeberg *et al.*, 1999).

Within-individual consistency of sexual display performance or ornamentation is important from the viewpoint of the signaller, as if individual attractiveness varies across, or even within breeding opportunities, it may not confer net fitness advantage to the male (Boake, 1989; Wagner & Sullivan, 1995). But it is also crucial for the receiver, as the degree and pathway of both additive genetic determination and condition-dependence determine the benefits from choosiness (Rowe & Houle, 1996).

Repeatability of a trait indicates the proportion of total variation that is because of differences between individuals (Falconer, 1989). In other words, it is the ratio of genetic and general environmental variance to total phenotypic variance, which means that it is an upper-bound estimate of heritability, the degree of additive genetic determination.

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Repeatability and heritability estimates presented together are very informative (Boake, 1989). Estimates do not always meet the theoretical requirements that repeatability always has to be larger than heritability. Small repeatability and large heritability estimates for a secondary sexual trait may indicate, for example, short-term, early environmental effects related to paternal expression of the character. In Norwegian pied flycatchers *Ficedula hypoleuca*, females prefer males with a more pronounced plumage contrast (Sætre *et al.*, 1994), which indicates paternal feeding propensity (Sætre *et al.*, 1995), which causes short-term resemblance of fathers and sons in this condition-dependent plumage trait (Slagsvold & Lifjeld, 1992). Small repeatability and small heritability suggest phenotypic plasticity (Wagner & Sullivan, 1995). Large repeatability and small heritability may indicate strong past selection and the resulting depletion of additive genetic variance (Boake, 1989) or pronounced, long-term early environmental effects on the character which are unrelated to parental expression of the trait (Doutrelant *et al.* 2000).

Large repeatability and large heritability strongly indicate additive genetic determination. This case, however, still includes two pathways, which are tentatively illustrated in Fig. 1. First, condition-dependent viability indicators may express high repeatability and, under certain circumstances, also high heritability, if some genes substantially affect adult body condition, and development of the trait is adjusted to state (good genes traits, Fig. 1a). Good examples are male and female tail length in the barn swallow *Hirundo rustica* (Møller, 1993, 1994; Pomiankowski & Møller, 1995) and male forehead patch size in Swedish collared flycatchers *F. albicollis* (Qvarnström, 1999a). Secondly, there are heritable display traits, the expression of which is regulated also by genes, but not adjusted to body condition (fixed traits, Fig. 1b), for instance, the orange spot pattern in male guppies *Poecilia reticulata* (Houde, 1992; Brooks, 2000), and plumage pattern in female barn owls *Tyto alba* (Roulin *et al.*, 1998; Roulin, 1999). Fixed traits may also indicate viability (Roulin *et al.*, 2000). In other cases, offspring of more ornamented males are more attractive, but less viable (Fisherian display traits, Pomiankowski & Iwasa, 1993; Wedell & Tregenza, 1999; Brooks, 2000).

Determination, role and costs of male forehead patch size in the two *Ficedula* sister species, pied (*F. hypoleuca*) and collared flycatchers (*F. albicollis*), have been the subject of increasingly detailed observation and experimentation during the last decade (Table 1). Norwegian pied flycatchers and Swedish collared flycatchers differ in both heritability and role of the ornament. This suggests, as proposed by Dale *et al.* (1999), that forehead patch size has lost its genetic variability in Norway, and this led to male rivals and females turning to other traits that better indicate genetic quality of their bearer. It would be very interesting to know, however, if changes in determination and role of an ornament can also happen indepen-

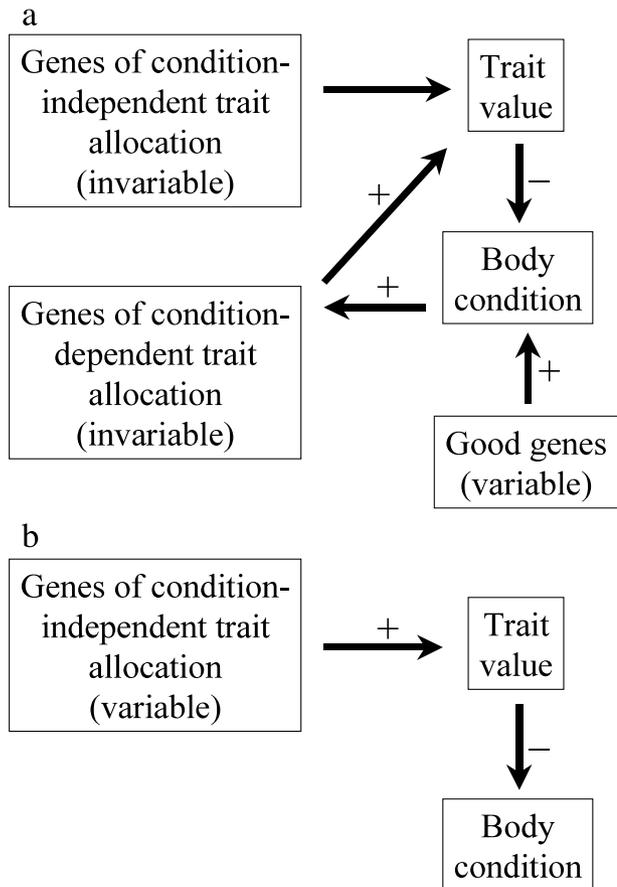


Fig. 1 The two main pathways of determination of sexually selected, heritable traits: condition-dependent 'good genes' signalling (a), and condition-independent (b).

Table 1 Published evidence on proximate determination, role, and costs of male forehead patch size in populations of two sister species: collared (*Ficedula albicollis*) and pied flycatchers (*F. hypoleuca*).

Species population	<i>Ficedula hypoleuca</i> Norway	<i>F. hypoleuca</i> Spain	<i>F. albicollis</i> Sweden
Condition-dependence	Yes ¹	Unknown	Yes ^{3,4,5}
Age-dependence	Yes ¹	Unknown	Yes ⁴
Heritability	No ¹	Unknown	Yes ⁵
Sexual selection	No ¹	Yes ²	Yes ^{4,6,7,8,9}
Maintenance costs	Unknown	Unknown	Yes ^{3,10,11}

¹Dale *et al.* (1999); ²Potti & Montalvo (1991a); ³Gustafsson *et al.* (1994); ⁴Gustafsson *et al.* (1995); ⁵Qvarnström (1999a); ⁶Pärt & Qvarnström (1997); ⁷Qvarnström *et al.* (2000); ⁸Sheldon *et al.* (1997); ⁹Sheldon & Ellegren (1999); ¹⁰Qvarnström (1997); ¹¹Qvarnström (1999b).

dently of each other. For example, do populations exist where the forehead patch size is sexually selected, but the degree or pathway (Fig. 1) of its additive genetic determination differs from that observed in Sweden? If so, this may have profound implications to our current

view on the interrelations between metabolic origin, signalling value, and role of ornamental traits.

In this paper, we investigate age- and condition-dependence, repeatability, and heritability of sexually selected forehead patch size, and its relationship to survival and longevity in a Central-European population of collared flycatchers, using 9 years of data. We show that the determination of this signal is different from that in Sweden: it is a fixed trait in our population, with high repeatability and heritability, but very small age- and no condition-dependence, and apparently with little viability-indicator value.

Methods

The collared flycatcher (*F. albicollis* Temm.) is a sexually dichromatic, socially monogamous, hole-nesting, migratory passerine. Females are greyish brown, with white wing patch and underparts. On the breeding plumage of males, which they grow at the complete winter molt, shiny black contrasts strongly with the white forehead patch, collar, wing patch and underparts (and not only for the human eye, Götmark & Hohlfält, 1995). For details on our study area and general field methods, see Török & Tóth (1988, 1999). Breeding phenology of collared flycatchers is described in Gustafsson (1989).

In our study population, approximately 10% of males are polygynous. The occurrence of monoterritorial polygyny (i.e. when there is no chance to conceal mating status, see Stenmark *et al.*, 1988) is limited to males with a large forehead patch (J. Török, G. Michl, L. Zs. Garamszegi & L. Tóth, unpublished results). Extra-pair mating activity of females increases with decreasing badge size of their social mate (Michl *et al.*, 2002). Thus, forehead patch size is sexually selected in our population.

The present analyses are based on male attractiveness and breeding data collected during the breeding seasons of 1990–1998. We recorded the largest height and width of forehead patches to the nearest 0.1 mm, with a caliper. Width and height are weakly positively correlated ($r^2 = 0.061$, $F_{1,1129} = 73.670$, $P < 0.0001$). As separate statistics for the two measures yielded virtually identical results, we used their product as an estimate of forehead patch size. Within-season repeated measurements ($n = 43$) by different combinations of the ringers who participated in the work give a measurement repeatability of 0.68 ± 0.14 SE. This is very close to that in the Swedish population (0.76 ± 0.10 , $n = 19$, A. Qvarnström, pers. comm.).

Our repeatability and heritability, as well as those of previous authors, may be underestimated for reasons other than measurement error. A within-season change in forehead patch size was recently demonstrated in the Swedish population (Griffith & Sheldon, 2001). We do not have enough data to evaluate correlates of within-season change in forehead patch size, so we cannot

address this problem in the present paper. None of the studies with which we compared our results did control for this potential source of error.

Males were trapped in the nestbox, measured and ringed if necessary when feeding young. Nestlings were measured and ringed at the age of 13 days. We measured tarsus length with a caliper, to the nearest 0.1 mm, and body mass with a Pesola® spring balance, to the nearest 0.1 g. The use of residuals from a weight/tarsus linear regression to estimate body condition has been justified for this species (Pärt, 1990).

Our dataset covers all males with a known forehead patch size from the nine breeding seasons ($n = 1131$ measurements from $n = 773$ males). To avoid pseudoreplication, males with more than one record were represented by their first measurement in the correlative dataset. As an estimate of repeatability, we report the slope of a least-squares linear regression for males measured twice. For individuals measured in more than two seasons, we calculated RI from variance components as described in Becker (1984) and Lessells & Boag (1987). Heritability was estimated as twice the slope of a son-father regression (Falconer, 1989). Data from more than one recruit with the same social father were averaged irrespective of whether they originated from the same brood or from different nests. Without early male badge-size manipulations and cross-fostering, these heritability values are potentially inflated (or deflated) by environmental, maternal and paternal effects related to male badge-size, so we have to be cautious when interpreting them.

Male ages are accurate in case of recruits and individuals who started as 1-year old (in subadult plumage). As most of our nestlings revisited as an adult (and not as a subadult) started breeding in the second year after fledging (92 of 133 in this dataset), unknown adult males were assigned an age of 2 years at their first appearance. Our conclusions do not change if omitting these males from the age-dependence analyses, so we report results based on the whole dataset.

We use breeding lifespan of males who first bred in 1990–1995 as an estimate of their viability. This means that survival was always checked using at least three seasons following the focal year. These values are reliable as breeding site fidelity is very high in this species (Gustafsson, 1989; Pärt, 1991), capture effort was high throughout, and we never recaptured a male who was not found for more than 2 years before. Breeding site fidelity in our study population is well demonstrated by the following example. There were 167 males who were measured in two seasons during the study period, irrespective of whether these seasons were consecutive or not. Only four of these were found on different nestbox plots in the two seasons, and these plots were always within a few hundred metres from each other. We therefore think that male survival status could be correctly assigned using our criteria.

We used Statistica 4.5 (StatSoft, Inc. 1994) package throughout. All tests are two-tailed. Data are presented as mean \pm SE unless otherwise stated.

Results

Forehead patch size (mm^2) in the 1990–1998 database ($n = 1131$ measurements) ranged from 33 to 126 (mean: 74.44, s.d.: 14.21) and was normally distributed. Forehead patch was very weakly correlated to body size (tarsus length; $r^2 = 0.004$, $F_{1,1127} = 4.110$, $P = 0.043$) which was, therefore, not corrected for in the subsequent analyses. There was a significant negative correlation between change and original value for two consecutive measurements on the same male between seasons ($B = -0.320$, $F_{1,168} = 28.757$, $r^2 = 0.146$, $P < 0.001$), so we included first badge size as a covariate in all analyses of badge size change.

Repeatability and heritability of forehead patch size

The regression dataset consisted of 167 males that were measured twice. The ANOVA database had 262 measurements from 51 males with three, 13 with four, nine with five and two with six data. Among within-season repeats one was randomly selected, the other omitted. Repeatability estimates of forehead patch area calculated by the two methods are similar (regression slope: 0.704 ± 0.054 , $r^2 = 0.510$, $F_{1,165} = 172.04$, $P < 0.001$, ANOVA: $RI = 0.745 \pm 0.024$, $F_{74,187} = 11.189$, $P < 0.001$).

Heritability of forehead patch size based on the whole set of son (or son-average) – father pairs was $2 \times 0.230 = 0.460 \pm 0.154$ (Fig. 2a, $r^2 = 0.067$, $F_{1,124} = 8.960$, $P < 0.01$). This is, however, clearly an underestimate, as extra-pair matings occur mainly among females of small-patched males (Michl *et al.*, 2002), and presumably with large-patched males (Sheldon & Ellegren, 1999). We tried to minimize this problem by omitting the three most likely extra-pair nestlings (very large own and small father forehead patch, indicated by arrows on Fig. 2a). As a result, the heritability estimate increased to 0.584 ± 0.146 ($r^2 = 0.117$, $F_{1,121} = 16.009$, $P < 0.001$).

Condition-dependence of forehead patch size

Within-season correlations are based on the first or only measurement of 745 of the 773 males, i.e. whose body mass, tarsus length, and exact date of measurement relative to laying of the first egg (phase hereafter) were known (see also Methods). We omitted measurements taken before the eighth day after laying of the first egg (approximately 1 day after the start point of incubation by females and the beginning of the presumable main extra-pair mating period of males), as they were few (22) and highly distorted the phase distribution. As among-year differences in badge area, body mass, tarsus length and phase were all significant (all $P < 0.01$), we first

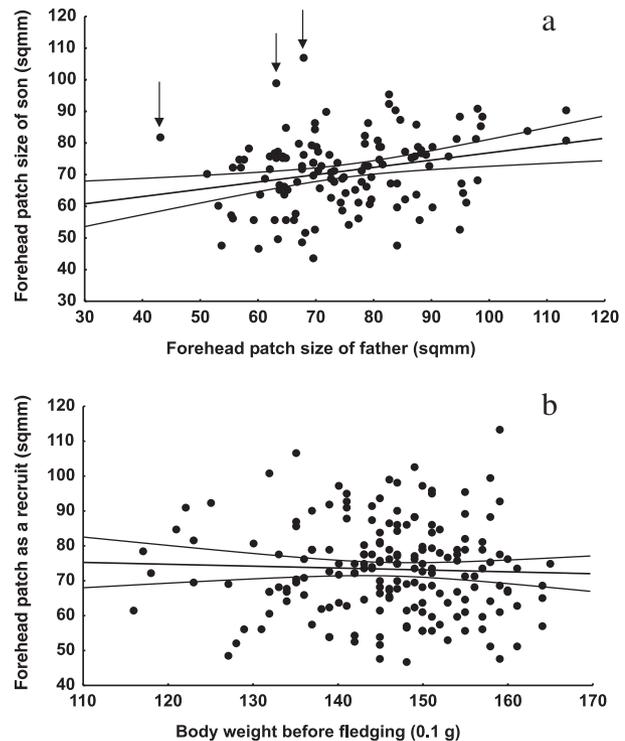


Fig. 2 Forehead patch size of male recruits in relation to father badge size (a) and development as a nestling (b). The three arrows indicate possible extra-pair offspring, see text.

standardized forehead patch size and phase, and calculated standard mass/tarsus residuals within each year. These data were pooled and entered into an analysis of covariance with body condition as a dependent variable, nest timing (early or late compared with mean standard laying date) and year as factors, and phase of breeding at measurement and badge size as covariates. From the final model 19 further cases were omitted as outliers (standard residual >3). This only influenced the magnitude of relationships and not their direction or significance, but normalized the distribution of standard phase-residual body condition values which were used during the following analyses. Body condition significantly decreased as breeding commenced (Fig. 3a, $\beta = -0.143$, $t_{684} = -3.789$, $P < 0.001$). There was, however, no relationship between forehead patch size and body condition (Fig. 3b, $\beta = 0.008$, $t_{684} = 0.221$, n.s.). Both relationships varied among years (ANCOVA, bivariate test of parallelism, $F_{16,668} = 3.656$, $P < 0.001$, both univariate tests significant), but both were unaffected by timing of breeding (early or late, $F_{2,682} = 1.759$, n.s., both univariate tests nonsignificant). The slope of the badge size/body condition relationship was negative in 4 and positive in 5 years.

Among those who returned and were measured the next year, next badge size was significantly related to the

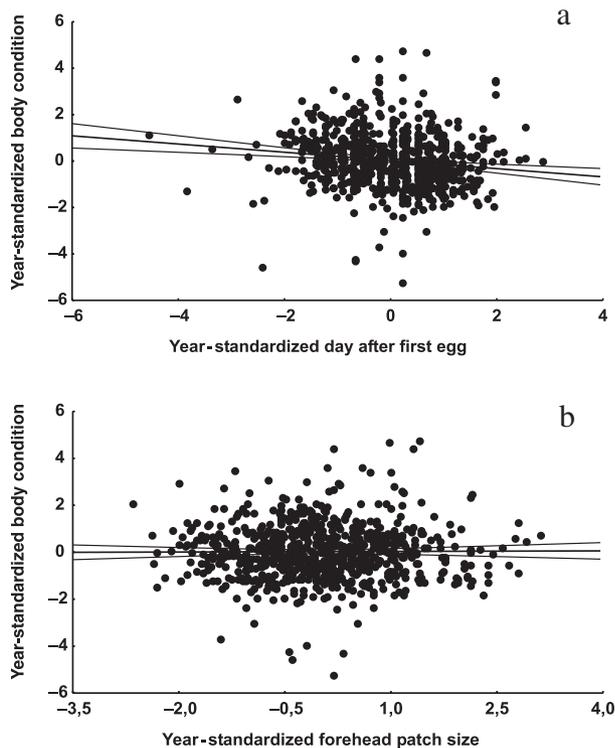


Fig. 3 Male body condition in relation to stage of breeding (a) and forehead patch size (b).

previous one (Fig. 4a, $\beta = 0.668$, $t_{132} = 10.420$, $P < 0.001$, also see above), but almost significantly negatively to phase-residual body condition during the previous season (Fig. 4b, $\beta = -0.118$, $t_{132} = -1.835$, $P = 0.069$), irrespective of year ($F_{14,110} = 0.578$, n.s.). Condition in the first season was also slightly negatively related to forehead patch size change (with first badge size as a covariate, $\beta = -0.163$, $t_{131} = -2.031$, $P = 0.044$). Slope did not vary significantly among seasons ($F_{14,110} = 0.578$, n.s.). Change in phase-residual condition between consecutive seasons did not predict change in badge area (with first badge size as a covariate, $\beta = 0.045$, $t_{128} = 0.546$, n.s.). There was a significant year effect on the direction of this relationship ($F_{14,107} = 1.849$, $P = 0.040$). The slope was positive in four of the eight and negative in the remaining four year pairs.

We also asked whether badge size change between seasons is related to original badge size. A within-season relationship is likely to reflect the effect of measurement error. In our case, the within-season slope ($B = -0.317$, $F_{1,41} = 5.185$, $r^2 = 0.112$, $P = 0.028$) was similar to that obtained between seasons ($B = -0.320$, see above). This suggests that, controlling for random measurement error, there is in fact no relationship between change and original value of forehead patch size.

Finally, we estimated the effects of development as a nestling on badge size as a recruit based on the heritability dataset (see Methods). In a multivariate regression

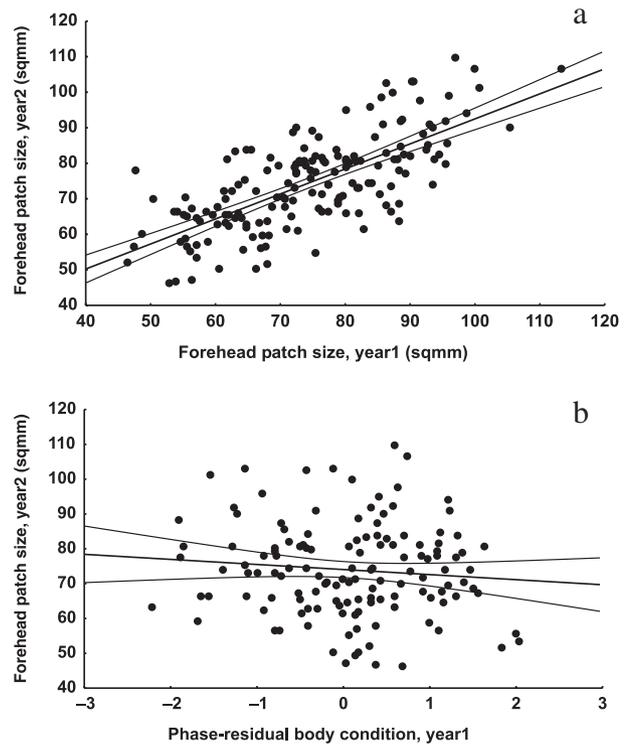


Fig. 4 Repeatability of forehead patch size (a) and its relationship to body condition the previous year (b).

model there was a significant effect of father badge size on offspring attractiveness ($\beta = 0.269$, $t_{108} = 2.903$, $P < 0.01$, also see above and Fig. 2a), but no correlation with body size or body weight at the age of 13 days (Fig. 2b, tarsus length $\beta = 0.015$, $t_{108} = 0.150$, n.s., body mass $\beta = -0.039$, $t_{108} = -0.403$, n.s.).

Age, age at first breeding, breeding lifespan, and forehead patch size

Males measured in two consecutive seasons (part of the regression repeatability dataset) were considered in the age-dependence tests. We created three classes based on age at first measurement: 1 year (subadult, 2Y), 2 years, and more than 2 years. The forehead patch was slightly smaller in subadult plumage than in the following year [means (s.d.): 72.47 (13.86) and 76.43 (17.11), respectively, paired $t_{32} = -2.473$, $P < 0.05$]. We did not observe patch size change between 2 and 3 years of age [73.75 (13.23) and 72.47 (13.10), paired $t_{76} = 0.933$, n.s.] or thereafter [78.94 (13.57) and 77.31 (11.27), $t_{27} = 0.915$, n.s.]. We also compared three age classes (2Y, 3Y, >3Y) within 8 year pairs using the whole dataset except within-year repeated measurements. The ANOVA was significant in only one of the year pairs, but even this significance vanished after sequential Bonferroni correction (data not shown).

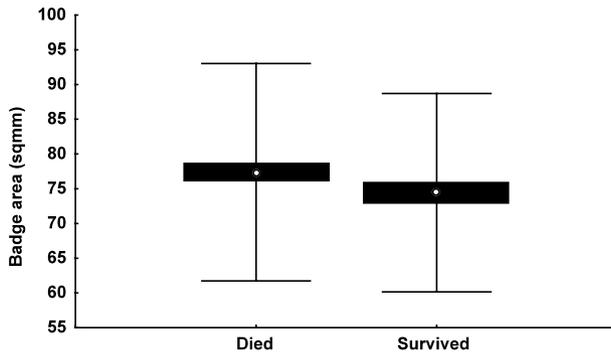


Fig. 5 Forehead patch size and survival of newly ringed adult males 1990–1995: mean \pm s.e., s.d.

The value of forehead patch size in predicting survival to the next breeding season was analysed on a sample of all measured males in 1990–1995 by separate logistic regressions for subadult and adult males. There was no relationship in second-year birds ($\chi^2 = 0.018$, d.f. = 1, n.s., $n = 69$ nonsurvivors and $n = 47$ survivors) but a negative tendency in adults (Fig. 5, $\chi^2 = 2.505$, d.f. = 1, $P = 0.113$, $n = 141$ nonsurvivors and $n = 83$ survivors). Breeding lifespan (categories: 1, 2, 3, or more years) was not associated with forehead patch area (two-way ANOVA, age at first breeding: $F_{1,332} = 0.376$, n.s., longevity: $F_{3,332} = 0.897$, n.s., interaction: $F_{3,332} = 0.362$, n.s.). This analysis also showed that males starting as a subadult have badge sizes similar to those breeding first as an adult.

Discussion

In this paper, we examined the proximate determination of sexually selected male forehead patch size in a Central-European population of the collared flycatcher. As the trait has been studied (Table 1) in a Swedish population on the island of Gotland, as well as in the sister species *F. hypoleuca*, our results can be placed in a comparative perspective.

In our population, repeatability analyses yielded larger values (0.70–0.74) than those obtained for the Swedish population (0.6, Qvarnström, 1999a), with small standard errors. As we used data from the whole breeding population, and from as many seasons per individual as possible, our estimates are unlikely to reflect sampling problems (Aragaki & Meffert, 1998; Catry *et al.*, 1999). The two methods of estimation (regression, ANOVA) yielded similar values. Given the measurement errors in the two populations (see Methods), this suggests that the ratio of variation in forehead patch size within males to that among individuals is slightly smaller than in the Swedish population.

When we corrected for the deflating effect of extra-pair paternity (Sheldon & Ellegren, 1999; Michl *et al.*, 2002), the already significant heritability of forehead patch size

increased to a value (0.58) much closer to the repeatability estimates. This is presumably still an underestimate, but it closely matches or exceeds values reported in the Swedish population (e.g. 0.04–0.36: Gustafsson, 1986; 0.44–0.65: Qvarnström, 1999a; 0.35–0.45: Merilä & Sheldon, 2000). Environmental effects on this heritability value (de Lope & Møller, 1993; Sætre *et al.*, 1995; Rossiter, 1996; Gil *et al.*, 1999; Griffith *et al.*, 1999) are likely to be absent, as judged from the condition-independence of badge size in this population.

In Sweden, forehead patch size increased with age (Gustafsson *et al.*, 1995). In Hungarian collared flycatchers, in contrast, the trait was strikingly stable during an individual male's life span. It did increase early in life, but within-year analyses failed to separate age classes based on the trait. Badge size did not show any decrease indicating senescence later in life, as it did in Norwegian pied flycatchers (Dale *et al.*, 1999). We found a near significant indication of survival cost of badge size among adult males, which is the age category presumably more seriously affected by male–male competition (Sætre & Slagsvold, 1996), which was proposed to be the main cost of this trait (Qvarnström, 1997). This tendency was present in 5 of the 6 years examined (data not shown). Negative relationship between a display trait and survival is not expected in case of condition-dependent expression.

In this long-distance migrant species, in contrast to resident *Parus* species, directional selection for higher body weight has been shown in an earlier study (Lindén *et al.*, 1992). This means that we cannot interpret the observed seasonal decrease of body condition as adaptive. The only explanation remaining is that reproduction is costly for males and body condition reflects this cost. The highly significant between-season repeatability of male body condition (0.802 ± 0.055 , $r^2 = 0.596$, $F_{1,160} = 236.06$, $P < 0.001$) also suggests that it is an appropriate measure of individual quality in our population, and a flexible ornament should reflect it (Rowe & Houle, 1996).

Badge size was unrelated to season-corrected body condition, and, in contrast to that in Sweden (Qvarnström, 1999b), this held irrespective of timing of breeding (early vs. late breeders). The significant year-effect on this relationship cannot be explained from the available data, but the fact that the slope was negative in four and positive in five seasons does not suggest a close causal link between body condition and forehead patch size in any direction. Subsequent forehead patch size and change in forehead patch size were slightly but consistently negatively related to previous body condition. This tendency is contrary to that expected under condition-dependence. Residual change in trait size from one year to the next was not related to change in body condition, which relationship was significantly positive on a much smaller dataset in Norwegian pied flycatchers (Dale *et al.*, 1999). The similarity of slopes of change/original regressions within and between years

indicates that there is in fact no relationship between badge size change and original value. This is also evidence for the lack of a phenotypic feedback mechanism. We checked all of these condition-dependence correlations for year effects. Where these were absent, the overall relationships were negative. Where a year effect was detected, negative slopes with $r^2 > 0.15$ frequently occurred. These are unlikely in case of condition-dependence, which is expected to produce positive or near-to-zero correlations in bad and good years, respectively.

The period after fledging is generally the most difficult to survive in small passerines (Weathers & Sullivan, 1989), and the role of body condition at fledging is crucial at these times (Tinbergen & Boerlijst, 1990; Lindén *et al.*, 1992). Condition-dependence of badge size could be most prominent in this sensitive period. In spite of our relatively large dataset (cf. for example, Slagsvold & Lifjeld, 1992; Møller, 1994; Dale *et al.*, 1999) and again in contrast to the Swedish data (Qvarnström, 1999a), we failed to find any relationship between fledgling state variables and recruit badge size. Thus, several lines of evidence lend support to the hypothesis that forehead patch size is not determined by body condition.

One could argue that costs of badge production and maintenance change in parallel to other costs of reproduction (Gustafsson *et al.*, 1995). Costs of reproduction can be difficult to detect, especially in favourable environments (among which some authors place nestbox plots, see Møller, 1989). This sometimes occurs even within a specific population (Tinbergen & Both, 1999). In such situations, phenotypic correlations do not necessarily reflect the real (constrained) allocation pattern which may be still present in the background. We consider this 'benign environment' explanation insufficient for the following reasons. First, even during the perhaps most demanding nestling-adult transition no trace of condition-dependence was found. Secondly, wing patch size, another heritable white plumage ornament, showed significant between-season condition-dependence and increased with age in our population, and it was positively related to survival chances beyond a certain age (J. Török, G. Hegyi, L. Zs. Garamszegi, submitted).

Thus forehead patch size in Hungarian collared flycatchers, unlike that in the Swedish population, seems to be unaffected by both development as a nestling and body condition as a parent, but shows high heritability and repeatability. We conclude that it is a condition-independent, heritable display trait (Fig. 1b). But what benefits do females acquire by choosing it?

Forehead patch size in Sweden is one of the best documented examples of good-genes indicator traits (Fig. 1a, Rowe & Houle, 1996). It is condition-dependent, repeatable and heritable (Qvarnström, 1999a), and seems to predict development of offspring in the absence of confounding maternal and paternal effects (Sheldon *et al.*, 1997). Condition-independent traits – such as badge size in our population – may (Roulin *et al.*, 2000) or may not

(Wedell & Tregenza, 1999; Brooks, 2000) confer genetic benefits other than offspring attractiveness. Large-patched adult males tended to survive poorly, but the relationship was not significant, and it was absent in subadults, so we cannot draw a firm conclusion in either direction. There is, however, an intriguing possibility that the signal conveys different information in the two populations, which should be investigated in more detail.

During the past years several studies convincingly demonstrated the existence of condition-independent display traits in various taxa (Houde, 1992; Etges, 1996; Roulin *et al.*, 1998; Wedell & Tregenza, 1999; Brooks, 2000). We have perhaps the most detailed information on geographical variation in determination and role of male coloration in the *Ficedula* species. There is a report of different determination of forehead patch size in two populations, but the trait is not sexually selected in one of these, and its additive genetic variance seems depleted (Dale *et al.*, 1999). Published results suggest that age and body condition may differently affect male plumage colour in different populations of the pied flycatcher (Potti & Montalvo, 1991b; Slagsvold & Lifjeld, 1992; Alatalo *et al.*, 1994), but data on both background and role of the trait are incomplete. In house finches (*Carpodacus mexicanus*) survival and fecundity selection slopes and interrelations among parts of a composite trait (carotenoid coloration) indirectly suggest differences in both determination and sexual selection between two populations (Badyaev *et al.*, 2001). To our knowledge, our results on collared flycatchers are the first to show that the same trait with the same importance in sexual selection may show the two qualitatively different pathways of additive genetic determination in two populations of a single species.

Further research is needed in both flycatchers and other taxa to reveal whether the within-species, within-trait difference in proximate determination suggested by our results is general. If it is, it will have several implications. For example, if the same trait can be under different developmental controls, then it may be hard to predict information content based on metabolic origin of signals (e.g. melanin, carotenoid, depigmented, see Badyaev & Hill, 2000). It may also be difficult to assess, based on one population, whether a signal is informative as an indicator of individual state or quality for conservation purposes (Grahn *et al.*, 1998). Models of trait-preference coevolution (Johnstone, 1996; Holland & Rice, 1998; Pomiankowski & Iwasa, 1998; Day, 2000) should incorporate possible change in trait determination with time, from condition-dependent to Fisherian and vice versa. Finally, it would be interesting to know whether this transition is generally in the direction predicted by Rowe & Houle (1996; condition-independent to condition-dependent) or the other way round, as originally proposed by Fisher (1930).

To summarize, in a Central-European population of the collared flycatcher male forehead patch size exhibited

large heritability and repeatability, but, in contrast to Swedish results, there was no evidence for any condition-dependence. It has not been demonstrated previously that proximate determination of the same heritable display trait with the same role may differ qualitatively between populations of a single species, which represents a new direction for observational, experimental, and modelling studies.

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