



## Phenotypic plasticity in a conspicuous female plumage trait: information content and mating patterns

GERGELY HEGYI\*†, BALÁZS ROSIVALL\*, ESZTER SZÖLLÖSI\*, RITA HARGITAI\*, MARCEL EENS† & JÁNOS TÖRÖK\*

\*Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University

†Department of Biology, University of Antwerp

(Received 10 January 2007; initial acceptance 16 February 2007;  
final acceptance 27 August 2007; published online 5 November 2007; MS. number: 9230R)

Explaining sexual ornamentation in the limiting sex, usually females, requires information on the proximate background of ornaments and their consequences for sexual selection. Phenotypic variation within individuals has received little attention in either of these research directions. We used 6 years of data to examine the information content and potential role of white wing patch size in female collared flycatchers, *Ficedula albicollis*. Female wing patch size differed among years. Yearling females had smaller wing patches than older females. The negative effect of original patch size on intraindividual patch size change was stronger in yearling than in older birds, which may reflect an age-dependent trade-off. Change in wing patch size was strongly positively related to the summer North Atlantic Oscillation (NAO) index. Clutch size laid in the previous breeding season had a negative effect on patch size change, but only in high-NAO years. Thus, the immediate effect of poor climate during moult apparently overrode the more indirect influence of reproductive effort. Two sexually selected ornaments of mates were unrelated to female wing patch size at the population level, but intraindividual changes of female wing patch size significantly predicted differences in wing patch size between mates obtained in the 2 years. Our data suggest that significant mating advantages to more ornamented females may not be detected from population-level mating patterns. Research on potential female ornaments should also pay more attention to age-dependent phenotypic plasticity, the trade-off between current and future ornament size and the costs of reproduction to apparent future attractiveness.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

**Keywords:** age; climate; collared flycatcher; female ornament; *Ficedula albicollis*; phenotypic plasticity; reproductive effort; sexual selection

For a long time, research on sexual selection focused almost exclusively on ornamentation of the sex with the usually higher potential reproductive rate, that is, males (Andersson 1994). However, it had already been emphasized in a very early phase of sexual selection research that the relative parental investment of the two sexes may affect the degree to which they are limiting to the other sex and can be choosy when mating, which allows females to play a role in sexual selection (Burley 1977).

*Correspondence:* G. Hegyi, Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University, Pázmány Péter sétány 1/C, H-1117 Budapest, Hungary (email: [everest@ludens.elte.hu](mailto:everest@ludens.elte.hu)). M. Eens is at the Department of Biology, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, 2610 Wilrijk, Belgium.

Burley also proposed that the more attractive an individual is, the choosier it can be towards the other sex. She found empirical evidence partly supporting these hypotheses by conducting mate choice tests among plumage morphs in pigeons (Burley 1977). Still, research on female ornamentation in species with conventional sex roles has been accumulating only slowly (Amundsen 2000).

One of the two theories explaining the existence of elaborate traits in females of species with conventional sex roles is genetic correlation with the corresponding ornament in males (Lande 1980). Studies testing this hypothesis have reached opposing conclusions, depending on whether they conducted interspecies comparisons (e.g. Irwin 1994; Omland 1997; Wiens 1999) or intraspecies comparisons (Price & Burley 1994; Price 1996; Roulin & Dijkstra 2003). The other of the two theories explaining mutual ornamentation is adaptive sexual selection in

both sexes (Cuervo et al. 1996). For example, the sex providing less parental care has more to lose by being choosy because the other sex is limiting, but it may also gain substantial benefits if the parental quality of the limiting sex varies among individuals and is important to reproductive success (Johnstone et al. 1996). Sexual selection on female ornaments has been suggested by laboratory and field experiments (Hill 1993; Amundsen et al. 1997; Griggio et al. 2005, but see Cuervo et al. 1996; Wolf et al. 2004) and by observations of significant patterns of assortative mating in the wild (Møller 1993; Roulin 1999; Kraaijeveld et al. 2004).

To support costly mate choice, female ornaments are expected to convey information on the quality of their bearer. There is surprisingly little evidence on the indicator value of sexually selected traits in females. It is widely accepted that indicators of age are advantageous to assess because age may predict parental skills (Desrochers 1992) or genetic quality via differential survival (Mauck et al. 2004). Female trait elaboration in some cases increases with age (Kraaijeveld et al. 2004; Jouventin et al. 2005; but see Amundsen et al. 1997; Siefferman & Hill 2005a). Ornaments indicating body condition may also convey both direct benefits (Radesäter & Jakobsson 1989; Palokangas et al. 1994) and indirect advantages via the 'good genes' process (Kotiaho et al. 2001; Parker & Garant 2004). Few studies have examined the dependence of conspicuous female traits on body condition, with mixed results (Johnsen et al. 1996; Jawor et al. 2004; Siefferman & Hill 2005a). Even more surprisingly, several studies examining the information content of potential female display traits did not look for indications of sexual selection (e.g. Piersma et al. 2001; Regosin & Pruett-Jones 2001; Mougeot et al. 2005), although it is evident that traits that have no role in sexual selection are not likely to reflect individual quality.

Some authors examined the relationship between conspicuous trait expression and body condition irrespective of the time of trait development (e.g. Amundsen et al. 1997; Jones et al. 2000; Velando et al. 2001), in which case the direction of causality is unclear (Jawor et al. 2004). Moreover, exaggerated traits may more seriously interfere with reproduction in females than in males, via conspicuousness to predators (Martin & Badyaev 1996), depletion of specific nutrients (Nordeide et al. 2006) or energetic trade-offs (Fitzpatrick et al. 1995). Although negative consequences of reproductive investment on future ornamentation have been repeatedly described in males (Gustafsson et al. 1995; Griffith 2000), females, the probably more affected sex, have rarely been examined in this respect (Johnsen et al. 1996). Finally, very few studies have documented the intraindividual changes of putative female ornaments over time (Muma & Weatherhead 1989; Johnsen et al. 1996). This makes it difficult to quantify phenotypic plasticity and to distinguish between direct and indirect benefits of choosing age-related traits. Moreover, apparent mating advantages are inherently hard to detect in population-level data such as the degree of assortative mating (Benton & Evans 1998). This problem is probably even more pronounced for potential mate choice signals in the limiting sex. Examining how changes in the

expression of exaggerated traits within individuals predict changes in the quality of mates obtained may represent a more powerful way of looking for sexual selection on female ornaments.

Here we examine the age dependence, condition dependence and apparent mating consequences of female wing patch size in collared flycatchers, *Ficedula albicollis*. The plumage of this species shows striking sexual dichromatism. The dorsal side of males is black, with prominent white forehead and wing patches and a white collar. Females are dull greyish brown above and lack the forehead patch and collar but have a white wing patch of size similar to that of subadult males. The relatively large yearly number of breeding pairs and the high site fidelity of individuals allow a reliable determination of age-related patterns and permit powerful intraindividual tests of the plasticity and mating correlates of female wing patch size because interyear mate fidelity is virtually absent in our study species (Gustafsson 1989).

The white plumage ornaments of males are well studied. The size of the forehead patch, an exclusively male ornament, is heritable but shows very little plasticity in our population (Hegyi et al. 2002, 2006a). The wing patch size of males is heritable, repeatable and age and condition dependent and appears to predict survival chances in some age classes (Török et al. 2003; Hegyi et al., 2007). Both male ornaments appear to play roles in sexual selection in this population (Michl et al. 2002; Garamszegi et al. 2006; Hegyi et al. 2006a). It is therefore plausible to examine whether female wing patch size conveys information similar to that of male wing patch size, and whether females with larger white patches acquire more ornamented mates.

Moreover, environmental conditions at the study area strongly fluctuate from year to year. On the one hand, this unpredictable fluctuation prevents females from optimizing the number of eggs they lay (Török et al. 2004). In the absence of individual optimization, we might expect that larger clutch sizes have costs to the future size of potential display traits in females (Fitzpatrick et al. 1995). On the other hand, year quality impinges on the dynamics of male ornamentation, with different environmental factors shaping the distribution of forehead patch size and wing patch size (Hegyi et al., 2007; also see Garant et al. 2004). It would be interesting to determine whether similar year effects are detectable on the wing patch size of females.

Cross-sectional age dependence may reflect either intraindividual change, or trait-related survival or movement (Gil et al. 2001; Török et al. 2003). Here we first look for differences in white patch expression between yearling and older females, and examine whether the difference is explained by intraindividual changes. Second, to assess the phenotypic plasticity of female wing patch size, we examine the intraindividual responses of the trait to clutch size in the previous breeding season and climatic conditions at moult. Finally, we examine whether intraindividual changes in female wing patch size predict interyear changes in the attractiveness of mates obtained, and investigate the consequences of any such apparent mating advantage to assortative mating at the population level.

As empirical and theoretical work shows that the information content and role of exaggerated traits may change with age (e.g. Proulx et al. 2002; Badyaev & Duckworth 2003), we take into account the age of females when investigating mating patterns and phenotypic plasticity.

## METHODS

### Field Methods

The collared flycatcher is a small, long-distance migratory, hole-nesting passerine. The species is socially monogamous with only few males attracting a secondary female (Gustafsson 1989; Garamszegi et al. 2004a). Extra-pair fertilizations are frequent (Sheldon & Ellegren 1999; Michl et al. 2002; Garamszegi et al. 2004b). A population has been studied in the Pilis Mountains, near Szentendre, Hungary since the early 1980s. The study area consists of several nestbox plots (approximately 800 nestboxes) established in different parts of the same oak woodland (see Török & Tóth 1988 for more details). Males arrive at the plots in the second half of April. Females usually arrive a few days later than males and soon settle with a male. Nest building and incubation are done by the female, whereas both sexes feed the young. The modal clutch size is six (usually four to eight), and the number of eggs laid is apparently not individually optimized in our population (Török et al. 2004).

Female wing patch size was measured in the breeding seasons of 2001–2006. Parents were usually caught at 8–10 days of chick age and ringed if necessary. We measured tarsus length to the nearest 0.1 mm with a calliper and body mass to the nearest 0.1 g with a spring balance. The forehead patch size of males was determined as the product of largest height and largest width measured with a calliper (nearest 0.1 mm; Hegyi et al. 2002). The wing patch size of both sexes was measured as the sum of lengths of white on the outer vanes of primaries four to eight (Török et al. 2003) with a calliper (nearest 0.1 mm). Only a subset of females was measured for wing patch size in 2001. Male binary age (yearling or older) was determined from the presence or absence of subadult plumage (Svensson 1992), whereas female binary age (yearling or older) was estimated based on ringing data, with yearling recruits and unknown females first caught as breeders classified as yearlings. To assess the error introduced by the age estimation of breeding females, we repeated the cross-sectional and longitudinal tests of age dependence by introducing binary origin (recruit or not) as a factor and all of its relevant interactions (see Results). Female wing patch size was unrelated to body size measured by tarsus length (linear regression on the first measurements of each individual:  $r^2 < 0.0001$ ,  $F_{1,982} = 0.02$ ,  $P = 0.880$ ). Male ornaments are also largely independent of body size (Hegyi et al. 2002; Török et al. 2003). Accordingly, body size was not considered in the cross-sectional analyses. Female tarsus length is, however, significantly related to intraindividual changes in wing patch size (see Results), so it is included in the models of wing patch size change. Before analyses, the sizes of white

patches in both sexes were corrected for systematic differences among measurers (Hegyi et al. 2006a). There were only nine cases when the same female paired with the same male in two seasons. These second pairings and female recaptures were omitted from the cross-sectional and longitudinal tests of mating patterns, respectively.

### Phenotypic Plasticity

The primaries bearing the wing patch are replaced during the complete postbreeding moult in summer, whereas the wing patch of yearlings is grown at the postjuvenile moult (Cramp & Perrins 1993; G. Heggi, J. Török, L.Z. Garamszegi, B. Rosivall, E. Szöllösi, E & R. Hargitai, personal observation). This implies that the wing patch size of both age classes is expected to reflect environmental conditions in summer. Indeed, a previous analysis on a larger data set of male ornaments, involving temperature and precipitation at the study area as well as summer and winter North Atlantic Oscillation (NAO) indexes (for more details on NAO, see Hurrell 1995; Stenseth et al. 2003), indicated that the strongest predictor of changes in male wing patch size irrespective of age was the mean summer NAO index from June to August (Hegyi et al., 2007). Therefore, we used the summer NAO as the single descriptor of environmental effects during moult in the present study. The summer NAO correlates with European weather (Lindholm et al. 2001; Zveryaev 2004) and with local weather at the study area (data recorded by the State Meteorological Service in Budapest, 30 km from the study site; values from June to August, for the period 1971–2005; general linear models: monthly mean temperature: month:  $F_{2,99} = 14.12$ ,  $P < 0.001$ ; NAO:  $F_{1,99} = 0.10$ ,  $P = 0.756$ ; month\*NAO:  $F_{2,99} = 3.59$ ,  $P = 0.031$ ; monthly cumulative precipitation: month:  $F_{2,101} = 0.77$ ,  $P = 0.465$ ; NAO:  $F_{1,103} = 4.49$ ,  $P = 0.037$ , negative relationship; month\*NAO:  $F_{2,99} = 2.38$ ,  $P = 0.098$ ).

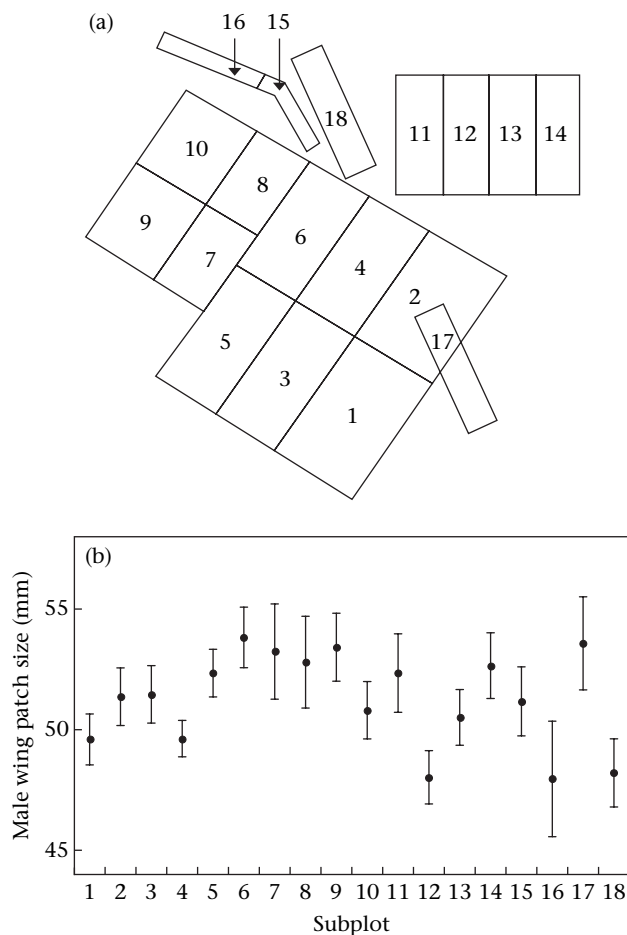
By using the summer NAO instead of several local factors, we could avoid false negative conclusions on environmental effects if birds moulted their wing patches after leaving the study area. Moreover, it has also been proposed that climatic indexes may be generally better predictors of population-level processes than local environmental variables because they capture a complex covariation among potentially several components of the environment (Hallett et al. 2004). We used the modified NAO index of Jones et al. (1997), obtained from <http://www.cru.uea.ac.uk/cru/data/nao.htm>.

In addition to testing the effects of environmental quality at the summer moult, we also investigated the influence of reproductive investment in the previous breeding season on the wing patch size of females. We used clutch size as an additional predictor of changes in wing patch size. Clutch size was corrected for date effects by also introducing laying date as a covariate in the analysis.

### Tests of Spatial Heterogeneity in Conspicuous Plumage Traits

In an additional analysis, we examined whether there was any consistent spatial structure in the distribution of

sexual ornamentation that may explain the lack of population-level assortative mating despite the apparent mating consequences of intraindividual changes in female wing patch size (see below and [Results](#)). We chose the central study plot system around the field station as the target of these tests for three reasons. First, this system holds a large proportion of our nestboxes ( $N = 315$ ) within a relatively limited area. Second, the area has a well-defined habitat structure, encompassing closed forest and clearings, areas with different densities of undergrowth, and both southern and northern slopes and a level plateau. Third, virtually all available breeding birds were caught on these plots in every year of the study. We chose an arbitrary subdivision ([Fig. 1a](#)) in which the 18 subplots were areas of rectangular shape parallel to the rows of the grids, had an approximately similar size and contained a similar number of nestboxes ( $17.50 \pm 1.04$  SE, range 10–29). We used data from the period 2002–2006 because female wing patch size was measured on only a subset of the population in 2001.



**Figure 1.** (a) Arbitrary subdivision of our central nestbox plots for the purpose of analysing the spatial heterogeneity of plumage patches in males and females. Numbers indicate individual subplots. (b) Differences among arbitrary nestbox subplots in the wing patch size of breeding males, excluding yearlings: means  $\pm$  SE.

## Statistical Methods

Throughout this paper, we used general linear mixed models with Satterthwaite correction, as implemented in the PROC MIXED of SAS 8.02 (SAS Institute, Inc., Cary, NC, U.S.A.). In the cross-sectional analyses, we used all measurements ( $N = 1454$ ) from all females ( $N = 978$ ) in the 6 years. However, missing data for different variables caused different sample sizes among tests. We assessed differences between yearlings and older birds by using wing patch size as a dependent variable, year and binary age as fixed factors, individual as a random factor and the year by age interaction. We looked for assortative mating by entering male ornament size as a dependent variable, year and female and male binary ages as fixed factors, female wing patch size as a covariate, female identity as a random factor and all interactions among female age, year and female wing patch size.

In the longitudinal analyses, we used all measurement pairs ( $N = 433$ ) where the female ( $N = 297$ ) was caught and its wing patch size measured in at least 2 consecutive years. However, sample sizes differ among analyses due to missing data. We analysed age dependence with wing patch size change as dependent variable, year and first year binary age as fixed factors, first year wing patch size and tarsus length as covariates, female identity as a random factor and all interactions among fixed effects except tarsus length. We assessed phenotypic plasticity with wing patch size change as dependent variable, first year binary age as fixed factor, first year wing patch size, tarsus length, first year summer NAO, first year clutch size and log-transformed laying date relative to the yearly median as covariates and year and female identity as random factors. We tested all relevant two- and three-way interactions. We investigated changes in mate quality in relation to changes in female wing patch size with change in male ornament size as dependent variable, year, the binary ages of first- and second-year males and the first year binary age of the female as fixed factors, first year ornament sizes of male and female and female tarsus length as covariates, and female identity as a random factor. We tested all relevant two- and three-way interactions.

In the spatial analysis, we compared the plumage patches of breeders among the subplots in general linear models with the given morphological attribute as dependent variable, subplot and year as fixed factors and the interaction of the two where possible. Separate models were run for the two sexes. Yearlings and older birds were also analysed separately because yearlings arrive later than older individuals and consequently occupy the places still vacant on the plots (Török et al. 2004; Hegyi et al. 2006b). Therefore, we did not expect the same spatial structure in the two age classes. The individual identity of birds was not taken into account in these calculations because the aim was to clarify the actual degree of spatial clustering in raw trait sizes. Interaction between year and subplot could not be calculated for yearlings because of their small number.

In all models, we used a stepwise backward elimination procedure, starting with the highest-order, least-significant effect. We made two exceptions to avoid the confounding



effects of background variables. Laying date was retained in the model together with clutch size even if it was not significant. Similarly, to control for the age dependence of male ornaments, male ages were always retained in the models of mating patterns. After stepwise removal, to avoid nonsignificance due to overparameterization, we re-entered all nonsignificant effects and interactions to the final model one by one and report these significances in the following. All *P* values are two tailed, and means are reported with their standard errors. We also report effect sizes (*r*) and their 95% confidence intervals with all significance estimates from general linear models. Effect sizes were calculated according to McNeil et al. (1996) and confidence intervals were computed with the macro Conf-Interval-r.sas (accessible at <http://core.ecu.edu/psyc/wuenschk/SAS/Conf-Interval-r.sas>).

## Ethical Note

Trapping and ringing of birds were conducted according to protocols established during the long-term monitoring of the study population of collared flycatchers since the early 1980s. An attempt was made to catch all breeding pairs in the population each year, but only a subset of females were measured for wing patch size in 2001. Accordingly, the number of females handled for this study ranged from 56 in 2001 to 389 in 2005, and the number of males ranged from 53 in 2001 to 344 in 2005. Birds were trapped with spring traps attached to the nestbox entrance and removed within a few minutes of trapping. All morphological and plumage measurements were done by experienced persons and did not take more than 3 min for either sex. The time required to measure wing patch size or forehead patch size was not more than 30 s, and neither measurement caused observable distress to the individuals. The birds were immediately released after measurements and resumed breeding activities soon thereafter. Work at the study site, including trapping and ringing birds, was done under permits from Duna-Ipoly National Park and the regional nature conservation authority: DINP 1255/2/2001, DINP 2256-3/2002, DINP 1931-2/2003, DINP 2573/2/2004, KTVF 15951/2005, KTVF 22021/2006.

## RESULTS

### Age Dependence and Repeatability

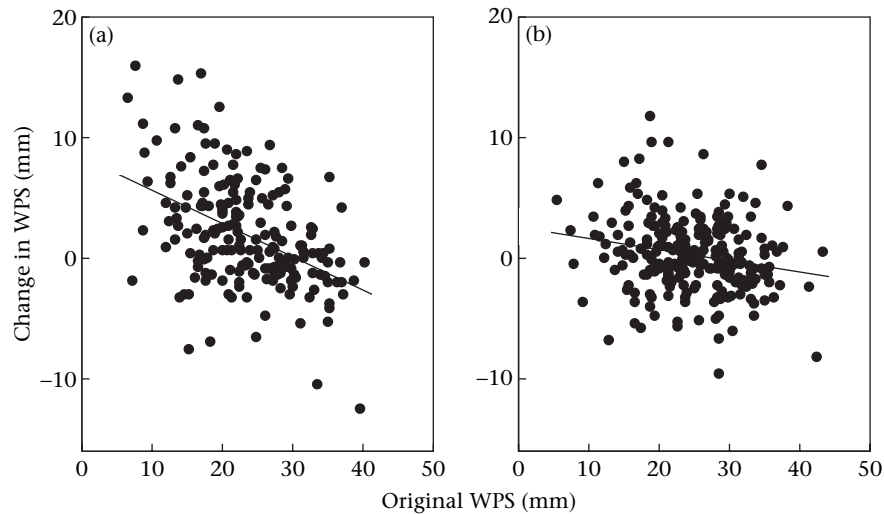
Female wing patch size ranged 2.7–50.2 mm (mean  $24.11 \pm 0.18$  mm,  $N = 1454$ ). Its coefficient of variance (CV) was 0.29, which is similar to that of male wing patch size (0.30), larger than that of male forehead patch size (0.21) and much larger than that of female tarsus length (0.03). In the cross-sectional data, female wing patch size differed between years ( $F_{5,737} = 7.13$ ,  $P < 0.001$ ,  $r = 0.215$ , CI lower = 0.165, CI upper = 0.264) and age classes ( $F_{1,1024} = 74.60$ ,  $P < 0.001$ ,  $r = 0.261$ , CI lower = 0.212, CI upper = 0.308), but there was no interaction between year and age ( $F_{5,944} = 1.32$ ,  $P = 0.255$ ,  $r = 0.083$ , CI lower = 0.032, CI upper = 0.134). Yearlings had smaller wing

patches ( $22.75 \pm 0.26$  mm,  $N = 682$ ) than older birds ( $25.30 \pm 0.25$  mm,  $N = 769$ ).

We also checked whether estimating age in some birds (nonrecruits) biased our conclusions. When entering the origin of the bird (recruit or not), its interaction with age, and the three-way interaction of origin, year and age in the model, the origin\*age interaction was significant ( $F_{1,777} = 29.66$ ,  $P < 0.001$ ,  $r = 0.192$ , CI lower = 0.142, CI upper = 0.241), indicating that estimated age is less accurate than known age. However, the interaction of age and year was not significant ( $F_{5,935} = 1.02$ ,  $P = 0.403$ ,  $r = 0.074$ , CI lower = 0.023, CI upper = 0.125). Moreover, the interaction of origin, age and year was also not significant ( $F_{15,841} = 1.25$ ,  $P = 0.232$ ,  $r = 0.148$ , CI lower = 0.097, CI upper = 0.198), indicating that the age- and year-related pattern of female wing patch size was not confounded by origin.

The interyear repeatability of female wing patch size was high ( $0.79 \pm 0.03$ ,  $F_{1,296} = 631.86$ ,  $P < 0.001$ , regression on raw data, first pair of measurements from each female). Change in female wing patch size was significantly predicted by year (mixed model with all data:  $F_{4,424} = 5.75$ ,  $P < 0.001$ ,  $r = 0.227$ , CI lower = 0.136, CI upper = 0.315), binary age ( $F_{1,424} = 27.82$ ,  $P < 0.001$ ,  $r = 0.248$ , CI lower = 0.157, CI upper = 0.334), tarsus length (negative effect,  $F_{1,424} = 7.23$ ,  $P = 0.008$ ,  $r = -0.129$ , CI lower = -0.221, CI upper = -0.035) and original wing patch size ( $F_{1,424} = 56.39$ ,  $P < 0.001$ ,  $r = -0.343$ , CI lower = -0.424, CI upper = -0.257). However, there was a significant interaction between binary age and original wing patch size ( $F_{1,424} = 18.04$ ,  $P < 0.001$ ,  $r = 0.202$ , CI lower = 0.110, CI upper = 0.291). Change and original wing patch size were significantly negatively related in both yearling and older females, but the relationship was much stronger in yearlings ( $F_{1,189} = 47.13$ ,  $P < 0.001$ ,  $r = -0.447$ , CI lower = -0.553, CI upper = -0.327) than in older birds ( $F_{1,231} = 6.99$ ,  $P = 0.009$ ,  $r = -0.171$ , CI lower = -0.292, CI upper = -0.045). Both age classes reduced their wing patch size after a year with very large patch size, but only yearlings showed a substantial increase in wing patch size after a year with small patch size (Fig. 2). Other interactions were nonsignificant ( $P > 0.221$ ). The variance of raw wing patch size changes was significantly higher in yearlings than in older females (Bartlett  $\chi^2_1 = 28.05$ ,  $P < 0.001$ ).

Considering origin (recruit or not) in the longitudinal model of age dependence revealed the same main patterns, with significant main effects of year ( $F_{4,422} = 5.89$ ,  $P < 0.001$ ,  $r = 0.230$ , CI lower = 0.139, CI upper = 0.317), age ( $F_{1,422} = 19.53$ ,  $P < 0.001$ ,  $r = 0.210$ , CI lower = 0.118, CI upper = 0.298), tarsus length ( $F_{1,422} = 6.56$ ,  $P = 0.011$ ,  $r = -0.124$ , CI lower = -0.216, CI upper = -0.030) and original wing patch size ( $F_{1,422} = 51.82$ ,  $P < 0.001$ ,  $r = -0.331$ , CI lower = -0.412, CI upper = -0.244) and a significant interaction between age and original patch size ( $F_{1,422} = 15.39$ ,  $P < 0.001$ ,  $r = 0.188$ , CI lower = 0.095, CI upper = 0.277). Although the effect of origin ( $F_{1,422} = 8.62$ ,  $P = 0.004$ ,  $r = 0.141$ , CI lower = 0.047, CI upper = 0.232) and its interaction with age were significant ( $F_{1,422} = 8.87$ ,  $P = 0.003$ ,  $r = 0.143$ , CI lower = 0.049, CI upper = 0.234), there was no interaction between origin and original wing patch size ( $F_{1,421} = 1.02$ ,  $P = 0.313$ ,



**Figure 2.** Change in the wing patch size (WPS) of (a) yearling and (b) older female collared flycatchers in relation to their original wing patch size. Least-squares regression lines are shown.

$r = 0.049$ , CI lower =  $-0.045$ , CI upper =  $0.143$ ) or between origin, binary age and original wing patch size ( $F_{2,420} = 2.63$ ,  $P = 0.073$ ,  $r = 0.111$ , CI lower =  $0.017$ , CI upper =  $0.203$ ), and all other interactions were nonsignificant ( $P > 0.396$ ). We therefore conclude that the effect of the use of females with estimated age on the detection of age-associated patterns is small, so we do not consider origin in the more complex analyses presented below. Finally, tests of female wing patch size changes using age as a continuous variable showed neither linear nor polynomial changes after 2 years of age (not shown), so the use of binary age is justified.

### Phenotypic Plasticity

The expanded analysis of intraindividual changes (Table 1) showed a similar effect of age, original wing patch size, and the age by original wing patch size interaction. In addition, summer NAO had a significant positive effect on wing patch size, irrespective of age or original wing patch size. The effect

of clutch size was not significant but showed a marginally significant interaction with summer NAO ( $P = 0.072$ ; Fig. 3). A separate analysis using a binary categorization of years based on median NAO showed that the effect of clutch size on wing patch size change was not significant in low-NAO years ( $F_{1,320} = 0.12$ ,  $P = 0.727$ ,  $r = 0.019$ , CI lower =  $-0.090$ , CI upper =  $0.127$ ) but significantly negative in high-NAO years ( $F_{1,91} = 4.27$ ,  $P = 0.042$ ,  $r = -0.212$ , CI lower =  $-0.398$ , CI upper =  $-0.010$ ). In a high-NAO summer, females substantially increased their wing patches if they laid a small clutch. In a low-NAO summer, however, females grew smaller patches irrespective of previous clutch size.

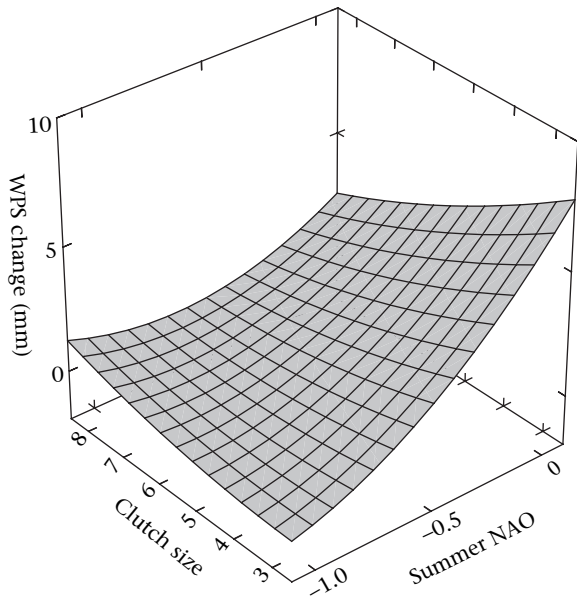
### Mating Advantages

At the population level, female wing patch size showed no relationship with either male wing patch size ( $F_{1,592} = 0.54$ ,  $P = 0.464$ ,  $r = 0.030$ , CI lower =  $-0.028$ , CI upper =  $0.088$ ) or male forehead patch size ( $F_{1,720} = 1.12$ ,  $P = 0.290$ ,  $r = 0.039$ , CI lower =  $-0.018$ , CI upper =  $0.095$ ).

**Table 1.** Intraindividual changes in the wing patch size of female collared flycatchers, in relation to original wing patch size, age, climate during the summer moult and previous clutch size

	<i>df</i>	<i>F</i>	Effect ( <i>r</i> )	CI lower	CI upper
Binary age	1,414	23.05***	0.229	0.137	0.329
Summer NAO index	1,414	13.69***	0.179	0.085	0.270
Tarsus length	1,414	8.68**	-0.143	-0.235	-0.048
WPS	1,414	51.44***	-0.332	-0.414	-0.244
Clutch size	1,412	1.14	-0.053	-0.148	0.043
Laying date	1,412	1.08	-0.051	-0.146	0.045
Age×summer NAO	1,413	0.90	0.047	-0.049	0.142
Age×WPS	1,414	15.14***	0.188	0.094	0.279
Age×clutch size	1,411	0.16	0.020	-0.076	0.115
Summer NAO×WPS	1,413	0.27	0.026	-0.070	0.121
Summer NAO×clutch size	1,411	3.25†	0.089	-0.007	0.183
Age×summer NAO×WPS	2,412	1.01	0.070	-0.026	0.165
Age×summer NAO×clutch size	2,410	1.76	0.092	-0.004	0.186

General linear mixed model with Satterthwaite correction and backward stepwise model selection. The random factors of female identity and year (both ns) are not shown here. WPS: wing patch size. † $P < 0.10$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; CI: 95% confidence interval.



**Figure 3.** Surface plot illustrating how the response of wing patch size (WPS) change within individual female collared flycatchers to clutch size laid in the previous breeding season depends on the NAO index at the summer moult. The surface was fit in Statistica 5.5.

Female age and all interactions in both models were non-significant ( $P > 0.150$ ). There are therefore no overall patterns that would suggest assortative mating in relation to the white patches. However, an intraindividual increase in female wing patch size was accompanied by a significant increase in the wing patch size of the mate obtained, irrespective of year and age (Table 2, Fig. 4). There was no such effect for changes in the forehead patch size of mates, and no interaction was significant in either model (Table 2).

## Spatial Patterns in the Plumage Traits of Males and Females

Spatial autocorrelation in sexual trait size may explain why the apparent mating advantage resulting from intraindividual increases in female wing patch size did not translate to population-level assortative mating. When testing this explanation using arbitrary subplots of our central study plot system, we detected a significant, temporally consistent spatial structure in the wing patch size of old males (Fig. 1b; see Table 3 for details). Of the 153 comparisons of pairs of subplots (LSD tests), 22 were significant, another 15 were marginal ( $P < 0.1$ ) and the remaining 116 were nonsignificant. There was no such spatial heterogeneity in the wing patch size of yearling males. Moreover, neither male forehead patch size nor female wing patch size showed consistent differences among subplots in either age class. The interaction between subplot and year was also not significant in any test.

## DISCUSSION

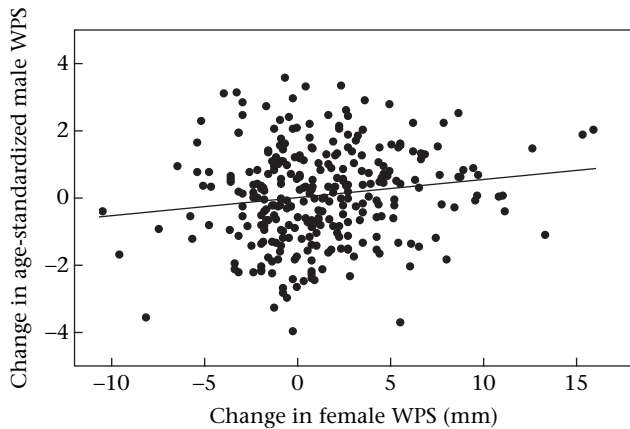
### Phenotypic Variation and Age Dependence

Female wing patch size showed a large phenotypic variance in our population. Its coefficient of variance was similar to that of male wing patch size despite the much smaller age dependence of female than male wing patch size (see below). The CV of female wing patch size was also considerably larger than that of male forehead patch size and an order of magnitude larger than that of an ordinary morphological trait (tarsus length). This large variability does not support species recognition as an explanation for the presence of wing patches in female

**Table 2.** Intraindividual changes in female collared flycatchers in the age-standardized ornamentation of the social mate obtained in two consecutive seasons

	Change in WPS of mate					Change in FPS of mate				
	df	F	Effect (r)	CI lower	CI upper	df	F	Effect (r)	CI lower	CI upper
Year	4,286	0.57	0.089	-0.007	0.183	4,308	3.57**	0.210	0.102	0.313
Female binary age	1,289	2.77	0.097	0.001	0.191	1,307	0.02	0.008	-0.103	0.118
Age of original male	1,290	0.00	0.000	-0.096	0.096	1,307	1.82	0.077	-0.034	0.186
Age of second male	1,290	535.70***	0.805	0.769	0.836	1,308	6.49*	0.143	0.034	0.251
Female tarsus length	1,289	1.10	-0.062	-0.157	0.034	1,307	0.53	-0.042	-0.152	0.069
Original male ornament size	1,290	257.03***	-0.685	-0.733	-0.631	1,308	321.91***	-0.715	-0.765	-0.656
Female WPS change	1,290	6.32*	0.146	0.051	0.238	1,307	1.60	-0.072	-0.181	0.039
Year×female age	4,281	1.73	0.155	0.06	0.247	4,303	1.42	0.136	0.026	0.243
Year×original male ornament	4,282	0.35	0.070	-0.026	0.165	4,300	1.63	0.146	0.036	0.252
Year×female WPS change	4,282	0.29	0.064	-0.032	0.159	4,303	0.36	0.069	-0.042	0.178
Female age×original male ornament	1,288	2.10	0.085	-0.011	0.179	1,306	0.25	0.029	-0.082	0.139
Female age×female WPS change	1,288	1.00	0.059	-0.037	0.154	1,305	2.72	0.094	-0.017	0.202
Year×female age×original male ornament	9,276	1.25	0.198	0.104	0.288	9,294	1.39	0.202	0.094	0.306
Year×female age×female WPS change	9,276	0.46	0.122	0.027	0.215	9,297	1.30	0.195	0.086	0.299

General linear mixed models with Satterthwaite correction and backward stepwise model selection. The random factor of female identity (ns in both cases) is not shown here. WPS: wing patch size; FPS: forehead patch size. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; CI: 95% confidence interval.



**Figure 4.** Differences in the wing patch size (WPS) of social mates obtained in two consecutive seasons, in response to changes in the wing patch size of individual female collared flycatchers. Yearling and older males differ qualitatively in wing patch size, so we use age-standardized male ornament sizes in this graph. The least-squares regression line is shown.

collared flycatchers (also see Wiley et al. 2005) and makes the trait likely subject to sexual selection.

Our cross-sectional data revealed that yearlings had smaller wing patches than older females, in line with many previous studies of conspicuous female traits (e.g. Potti & Merino 1996; Regosin & Pruett-Jones 2001; Jouventin et al. 2005). Age may indicate phenotypic quality in terms of body condition, experience or arrival date (Wiebe & Martin 1998; Ferrer & Bisson 2003; Williams & Christians 2003) or genetic quality, if quality is positively related to survivorship (Wooller et al. 1990; Cam & Monnat 2000; Mauck et al. 2004). The mean difference in wing patch size of 2.55 mm in the two age classes (see Results) is largely explained by the observed intraindividual increase of the trait after 1 year of age ( $1.94 \pm 0.27$  mm), which does not support the survival-indicator mechanism in our population. In the case of survival effects, we would expect a substantial residual age difference in absolute wing patch size even after controlling for intraindividual changes. However, mark–recapture studies are needed to examine this topic in more detail (e.g. Jones et al. 2004).

We found a significant but moderate increase in wing patch size in yearling females, whereas males of the same age approximately double their wing patch size (Török et al. 2003). This sex difference may reflect that the wing plumage of males is part of the subadult plumage and changes qualitatively between 1 and 2 years of age (Svensson 1992; Hegyi et al. 2006b), whereas there is no subadult plumage in females. The horizontal data also revealed significant interyear fluctuations in female wing patch size. We cannot rule out a systematic directional change in trait size due to selection (Møller & Szép 2005; Hegyi et al. 2006a) or nonrandom settlement patterns (Postma & van Noordwijk 2005). However, the strong effect of year-specific macroclimatic variation on change in wing patch size irrespective of original patch size suggests that at least part of the interyear variation in trait size may be due to consistent intraindividual changes.

**Table 3.** Comparisons of the white plumage patches of male and female collared flycatchers among arbitrary subplots of a nestbox grid system

Trait	Subplot			Year			Subplot×year			
	df	F	Effect (r)	CI lower	CI upper	df	F	Effect (r)	CI lower	CI upper
MWPS, 2Y	17,131	0.69	0.287	0.134	0.426	4,148	3.887**	0.308	0.157	0.445
MWPS, 2+	17,452	1.68*	0.244	0.157	0.327	4,448	1.511	0.115	0.025	0.203
MFPS, 2Y	17,147	0.81	0.293	0.147	0.427	4,160	0.270	0.082	-0.072	0.232
MFPS, 2+	17,477	1.53	0.227	0.142	0.309	4,490	1.786	0.130	0.042	0.216
FWPS, 2Y	17,301	0.79	0.207	0.100	0.309	4,318	3.231*	0.198	0.091	0.301
FWPS, 2+	17,443	0.58	0.148	0.057	0.236	4,456	0.937	0.090	-0.001	0.180
						68,371	1.190	0.423	0.345	0.495
						68,405	1.017	0.382	0.304	0.455
						68,380	0.894	0.371	0.290	0.446
								NA		

General linear models with backward removal and reintroduction. F values are shown with effect and error degrees of freedom. M: male; F: female; WPS: wing patch size; FPS: forehead patch size; 2Y: yearlings; 2+: older birds; NA: not applicable. \*P < 0.05; \*\*P < 0.01; CI: 95% confidence interval.



The relatively few studies examining intraindividual changes in conspicuous female traits usually found increase in trait size with age (Muma & Weatherhead 1989; Møller 1991; Johnsen et al. 1996). For female wing patch size, we found a strong interaction between age and original patch size in determining patch size change. In any test when the dependent variable is change in a trait with random measurement error, it is straightforward to control for original trait size because a large proportion of the variance in change will be explained by regression to the mean (Kelly & Price 2005). In our case, however, the age difference in slopes suggests that measurement error does not completely explain the relationship between the change and the original value of ornaments. This is further supported by the highly significant age dependence of the variance of raw wing patch size changes. After a year with a small patch, yearling females are capable of increasing their wing patch size to a far greater extent than older females. However, the two age classes suffer a similar reduction in wing patch size after growing a very large patch. This suggests that the future patch size costs of a large wing patch are more severe for yearlings than for older birds. Further, preferably experimental studies are needed that look for trade-offs between the current and the future sizes of potential female display traits (Møller 1989; Hegyi et al. 2002; Cuervo et al. 2003) in a way similar to life history research (Pettifor et al. 2001; Török et al. 2004).

### Condition Dependence

Studies in a variety of species have indicated that exaggerated female plumage traits reflected the body condition of their bearer. Some studies found correlations between trait size and body condition at capture (Rohde et al. 1999; Griggio et al. 2005; Mänd et al. 2005), which may reflect an effect of elaboration on body condition if the trait correlates with social dominance (Senar 1999; Jawor et al. 2004). Other studies reported or manipulated body condition during trait development (Jawor et al. 2004; Siefferman & Hill 2005a) or in a particularly stressful period before trait development (Johnsen et al. 1996). Looking for effects of year quality on trait expression may be a particularly powerful way of showing phenotypic plasticity (Johnsen et al. 1996; Jones et al. 2000) because such effects are often unpredictable and affect large groups of individuals in the same way. We found that, similar to male wing patch size dynamics (Hegyi et al., 2007), a large percentage of variation in intraindividual wing patch size change in females was explained by values of the NAO index during the summer moult of the ornament. High NAO indicates low precipitation in the study area, and probably in the larger area where our birds undergo their summer moult. The increase of wing patch size in females moulting under high NAO may therefore reflect better insect food availability in less rainy weather (Bryant 1975; Turner 1982).

The reproductive success of individuals is strongly constrained by the costs of reproductive effort in both the

short and the long term (reviews in Dijkstra et al. 1990; Roff 2001). Costs may be manifested in reduced survival (Daan et al. 1996; Orell & Belda 2002) or impaired future reproductive output (Pettifor et al. 2001; Török et al. 2004). It is widely recognized that reproductive effort may restrict subsequent sexual advertisement in males (Gustafsson et al. 1995; Griffith 2000; Siefferman & Hill 2005b). Although the theory of reproductive costs in terms of attractiveness was soon extended to females (Fitzpatrick et al. 1995), only a single study has addressed this topic in birds (Johnsen et al. 1996) and detected negative effects of the number of chicks reared on badge colour in female red-winged blackbirds, *Agelaius phoeniceus*. Here we correlatively explored the effect of reproductive effort on changes in a potential plumage signal of female collared flycatchers in a multivariate context. We found that the costs of reproduction as described by date-corrected clutch size were manifested only in females moulting under high NAO, that is, good conditions. It is important to note that large-scale summer climate may be largely independent of environmental conditions during the preceding spring breeding attempt, and the latter do not appear to affect clutch size in our population (Török et al. 2004). Therefore, the interactive effect of clutch size and summer NAO on female wing patch size may be due to the more proximate influence of a poor moult environment overriding reproductive costs in low-NAO summers. More specifically, Fig. 3 shows that, irrespective of clutch size, very few females could improve their wing patch size under low-NAO conditions. In a good moult environment, however, females that had invested little in reproduction showed a consistent increase in wing patch size. Our present data suggest that the effects of primary reproductive effort on female wing patch size may contribute to the fluctuating pattern of selection on clutch size in our population (Török et al. 2004) and support the opinion that the expression of potential display traits in females results from complex, resource-dependent allocation decisions at multiple stages of the yearly cycle (Fitzpatrick et al. 1995).

### Mating Patterns

In mutual ornamentation systems, it is plausible to expect that more ornamented members of any sex have more opportunity to choose among potential mates (Johnstone et al. 1996). In this case, the attractiveness of an individual should predict the attractiveness of its mate, as shown in several species (e.g. Møller 1993; Linville et al. 1998; Safran & McGraw 2004). However, the situation may become more complex if attractiveness is a function of multiple factors, for example, ornamentation and age. Here we correlatively examined the patterns of male and female plumage patches on two levels. Population-level relationships between female wing patch size and either wing patch size or forehead patch size of its mate were not significant. However, the changes of the wing patch size of an individual female from one year to the next significantly predicted differences in the wing patch size of its consecutive mates. Age-assortative mating does not explain this pattern because we allowed for

binary age in our statistical analysis, and neither male ornaments (Hegyi et al. 2002; Török et al. 2003) nor female wing patch size changed systematically after 2 years of age (mean female wing patch size change 0.28 mm, 95% CI lower  $-0.20$ , upper 0.76). Arrival or breeding date may also confound mating patterns. However, change in laying date relative to the yearly median did not contribute significantly to the model of the wing patch size changes of mates ( $P = 0.778$ ), and the effect of female wing patch size remained almost quantitatively identical with change in laying date as a covariate ( $P = 0.030$ ). It is therefore possible that the positive relationship between the changes in female wing patch size and male wing patch size is due to mutual sexual selection. However, we cannot rule out that the pattern we observed was caused by an unmeasured female trait that correlated with wing patch size, so experimental tests are necessary to reinforce this conclusion. It is nevertheless interesting that the apparent mating advantage of large-patched females was manifested in male wing patch size but not in male forehead patch size. Such a difference may be expected, however, given that wing patch size reflects the body condition and viability of males, whereas forehead patch size is not a reliable indicator of phenotypic quality in our population (Hegyi et al. 2002, 2006a, 2007; Török et al. 2003). An alternative explanation for the patterns is that wing patch size or a correlated trait may play a role in female competition for mating opportunities (Dale & Slagsvold 1995; Král et al. 1996), and the intensity of competition may depend on male attractiveness.

An important question is why the pattern in intraindividual female patch size changes did not translate to assortative mating on the population level. This may be due to the spatially restricted settlement and mate choice process of flycatchers (e.g. Dale et al. 1990; Potti & Montalvo 1991; Doligez et al. 1999). If both females and males show interyear fidelity to a breeding area, the set of males displaying and females prospecting in the neighbourhood of a given individual female should be consistent across years. Females are known to sample only a few males around the site of their arrival (Dale et al. 1990; Potti & Montalvo 1991). This implies that an increase in female wing patch size from one year to the next may lead to an improvement of mate quality due to intra- or intersexual selection. On the other hand, if females sample only a small subset of males in the population, systematic differences in the ornamentation of these spatially restricted subsets (for example due to territoriality; Pärt & Qvarnström 1997) may swamp the local correlation of female and male ornamentation at the population level, making it impossible to detect assortative mating (Benton & Evans 1998).

Our preliminary analysis of subplots supported these arguments by showing a temporally consistent spatial pattern in male wing patch size. This pattern may originate from the known role of the trait in territorial competition (Garamszegi et al. 2006) because competition may translate habitat quality patterns to male ornamentation patterns. Our analysis was extremely conservative because it explored a single spatial scale, and the borders of the arbitrary subplots were mostly

independent of actual differences in habitat quality as perceived by the birds. We conclude that females returning to breed near their previous year nestbox (Pärt & Gustafsson 1989) find a nonrandom subset of male wing patch size similar to that in the previous year. Therefore, females increasing their wing patch size from one year to the next may acquire a male of larger wing patch size within this subset, but these local advantages may not necessarily appear at the population level. Female competition explanations are apparently not supported by our data because female wing patch size showed no spatial heterogeneity within the area examined. In sum, our results suggest that more detailed investigations of mating patterns could greatly improve our knowledge of sexual selection in natural populations with site fidelity.

## CONCLUSIONS

Our results suggest that the wing patch size of female collared flycatchers is a highly variable and plastic trait. Intraindividual changes in the trait appear to reflect a complex interplay among original trait size, age, reproductive effort and environmental conditions during moult. These processes may explain most of the differences in female wing patch size in age classes and among years found in the cross-sectional analysis. These results suggest that the phenotypic plasticity of wing patch size changes with age (also see Badyaev & Duckworth 2003). Female wing patch size apparently conferred a mating advantage to females due to mutual choice or female competition because females increasing their patch size between 2 consecutive years paired with males with larger wing patch size in the second year. However, these mating dynamics were not detectable in population-level patterns of assortative mating.

Results of our study are in line with evidence that exaggerated plumage traits may be informative indicators of individual quality in females (Amundsen 2000) but also indicate that the function of potential display traits and the pathways through which these traits reveal quality deserve much more attention than they have received so far. In particular, future studies of conspicuous female traits should focus on the costs of reproductive effort (Fitzpatrick et al. 1995) and current trait size (Møller 1989) to future trait size, the age dependence of trait information content (Proulx et al. 2002) and the detailed background of large-scale mating patterns (Benton & Evans 1998). In our study species, further investigations should support our correlative suggestions with experimental data, enlighten the quantitative genetics of female wing patch size and examine its relationship with offspring quality, reproductive success and survivorship.

## Acknowledgments

We are grateful to L. Z. Garamszegi, M. Herényi, G. Michl, B. Szigeti and several students for help with the field work. L. Z. Garamszegi and two anonymous

referees kindly commented on previous versions of the paper. Our research was supported by OTKA Grants T34880, T49650 and T49678, a visiting postdoc grant from the University of Antwerp, several FWO grants (Flanders, Belgium), the Erdők a Közjóért Alapítvány and the Pilis Park Forestry.

## References

- Amundsen, T. 2000. Why are female birds ornamented? *Trends in Ecology & Evolution*, **15**, 149–155.
- Amundsen, T., Forsgren, E. & Hansen, L. T. T. 1997. On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society of London, Series B*, **264**, 1579–1586.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Badyaev, A. V. & Duckworth, R. A. 2003. Context-dependent sexual advertisement: plasticity in development of sexual ornamentation throughout the lifetime of a passerine bird. *Journal of Evolutionary Biology*, **16**, 1065–1076.
- Benton, T. G. & Evans, M. R. 1998. Measuring mate choice using correlation: the effect of female sampling behaviour. *Behavioral Ecology and Sociobiology*, **44**, 91–98.
- Bryant, D. M. 1975. Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance. *Ibis*, **117**, 180–214.
- Burley, N. 1977. Parental investment, mate choice, and mate quality. *Proceedings of the National Academy of Sciences, U.S.A.*, **74**, 3476–3479.
- Cam, E. & Monnat, J.-Y. 2000. Stratification based on reproductive state reveals contrasting patterns of age-related variation in demographic parameters in the kittiwake. *Oikos*, **90**, 560–574.
- Cramp, S. & Perrins, C. M. 1993. *The Birds of the Western Palearctic*. Vol. VII. Oxford: Oxford University Press.
- Cuervo, J. J., de Lope, F. & Møller, A. P. 1996. The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behavioral Ecology*, **7**, 132–136.
- Cuervo, J. J., Møller, A. P. & de Lope, F. 2003. Experimental manipulation of tail length in female barn swallows (*Hirundo rustica*) affects their future reproductive success. *Behavioral Ecology*, **14**, 451–456.
- Daan, S., Deerenberg, C. & Dijkstra, C. 1996. Increased daily work precipitates natural death in the kestrel. *Journal of Animal Ecology*, **65**, 539–544.
- Dale, S. & Slagsvold, T. 1995. Female contests for nest sites and mates in the pied flycatcher *Ficedula hypoleuca*. *Ethology*, **99**, 209–222.
- Dale, S., Amundsen, T., Lifjeld, J. T. & Slagsvold, T. 1990. Mate sampling behaviour of female pied flycatchers: evidence for active mate choice. *Behavioral Ecology and Sociobiology*, **27**, 87–91.
- Desrochers, A. 1992. Age and foraging success in European blackbirds: variation between and within individuals. *Animal Behaviour*, **43**, 885–894.
- Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. & Zijlstra, M. 1990. Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *Journal of Animal Ecology*, **59**, 269–285.
- Doligez, B., Danchin, E., Clobert, J. & Gustafsson, L. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology*, **68**, 1193–1206.
- Ferrer, M. & Bisson, I. 2003. Age and territory-quality effects on fecundity in the Spanish imperial eagle (*Aquila adalberti*). *Auk*, **120**, 180–186.
- Fitzpatrick, S., Berglund, A. & Rosenqvist, G. 1995. Ornaments or offspring: costs to reproductive success restrict sexual selection processes. *Biological Journal of the Linnean Society*, **55**, 251–260.
- Garamszegi, L. Z., Török, J., Michl, G. & Møller, A. P. 2004a. Female survival, lifetime reproductive success and mating status in a passerine bird. *Oecologia*, **138**, 48–56.
- Garamszegi, L. Z., Møller, A. P., Török, J., Michl, G., Péczely, P. & Richard, M. 2004b. Immune challenge mediates vocal communication in a passerine bird: an experiment. *Behavioral Ecology*, **15**, 148–157.
- Garamszegi, L. Z., Rosivall, B., Hegyi, G., Szöllösi, E., Török, J. & Eens, M. 2006. Determinants of male territorial behavior in a Hungarian collared flycatcher population: plumage traits of residents and challengers. *Behavioral Ecology and Sociobiology*, **60**, 663–671.
- Garant, D., Sheldon, B. C. & Gustafsson, L. 2004. Climatic and temporal effects on the expression of secondary sexual characters: genetic and environmental components. *Evolution*, **58**, 634–644.
- Gil, D., Cobb, J. L. S. & Slater, P. J. B. 2001. Song characteristics are age dependent in the willow warbler, *Phylloscopus trochilus*. *Animal Behaviour*, **62**, 689–694.
- Griffith, S. C. 2000. A trade-off between reproduction and a condition-dependent sexually selected ornament in the house sparrow *Passer domesticus*. *Proceedings of the Royal Society of London, Series B*, **267**, 1115–1119.
- Griggio, M., Valera, F., Casas, A. & Pilastro, A. 2005. Males prefer ornamented females: a field experiment of male choice in the rock sparrow. *Animal Behaviour*, **69**, 1243–1250.
- Gustafsson, L. 1989. Collared flycatcher. In: *Lifetime Reproduction in Birds* (Ed. by I. Newton), pp. 75–89. London: Academic Press.
- Gustafsson, L., Qvarnström, A. & Sheldon, B. C. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature*, **375**, 311–313.
- Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M. & Grenfell, B. T. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather? *Nature*, **430**, 71–75.
- Hegyi, G., Török, J. & Tóth, L. 2002. Qualitative population divergence in proximate determination of a sexually selected trait in the collared flycatcher. *Journal of Evolutionary Biology*, **15**, 710–719.
- Hegyi, G., Török, J., Tóth, L., Garamszegi, L. Z. & Rosivall, B. 2006a. Rapid temporal change in the expression and age-related information content of a sexually selected trait. *Journal of Evolutionary Biology*, **19**, 228–238.
- Hegyi, G., Rosivall, B. & Török, J. 2006b. Paternal age and offspring growth: separating the intrinsic quality of young from rearing effects. *Behavioral Ecology and Sociobiology*, **60**, 672–682.
- Hegyi, G., Török, J., Garamszegi, L. Z., Rosivall, B., Szöllösi, E. & Hargitai, R. 2007. Dynamics of multiple sexual signals in relation to climatic conditions. *Evolutionary Ecology Research*, **9**, 905–920.
- Hill, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the house finch. *Evolution*, **47**, 1515–1525.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, **269**, 676–679.
- Irwin, R. E. 1994. The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness. *American Naturalist*, **144**, 890–907.
- Jawor, J. M., Gray, N., Beall, S. M. & Breitwisch, R. 2004. Multiple ornaments correlate with aspects of condition and behaviour in female northern cardinals, *Cardinalis cardinalis*. *Animal Behaviour*, **67**, 875–882.
- Johnsen, T. S., Hengeveld, J. D., Blank, J. L., Yasukawa, K. & Nolan, V., Jr. 1996. Epulet brightness and condition in female red-winged blackbirds. *Auk*, **113**, 356–362.

- Johnstone, R. A., Reynolds, J. D. & Deutsch, J. C. 1996. Mutual mate choice and sex differences in choosiness. *Evolution*, **50**, 1382–1391.
- Jones, P. D., Jonsson, T. & Wheeler, D. 1997. Extension to the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and south-west Iceland. *International Journal of Climatology*, **17**, 1433–1450.
- Jones, I. L., Hunter, F. M. & Fraser, G. 2000. Patterns of variation in ornaments of crested auklets *Aethia cristatella*. *Journal of Avian Biology*, **31**, 119–127.
- Jones, I. L., Hunter, F. M., Robertson, G. J. & Fraser, G. 2004. Natural variation in the sexually selected feather ornaments of crested auklets (*Aethia cristatella*) does not predict future survival. *Behavioral Ecology*, **15**, 332–337.
- Jouventin, P., Nolan, P. M., Örnborg, J. & Dobson, F. S. 2005. Ultraviolet beak spots in king and emperor penguins. *Condor*, **107**, 144–150.
- Kelly, C. & Price, T. D. 2005. Correcting for regression to the mean in behaviour and ecology. *American Naturalist*, **166**, 700–707.
- Kotiaho, J. S., Simmons, L. W. & Tomkins, J. L. 2001. Towards a resolution of the lek paradox. *Nature*, **410**, 684–686.
- Kraaijeveld, K., Gregurke, J., Hall, C., Komdeur, J. & Mulder, R. A. 2004. Mutual ornamentation, sexual selection, and social dominance in the black swan. *Behavioral Ecology*, **15**, 380–389.
- Kráľ, M., Sætre, G. P. & Bicić, V. 1996. Intrasexual aggression of female collared flycatchers (*Ficedula albicollis*): competition for male parental care? *Folia Zoologica*, **45**, 153–159.
- Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **34**, 292–305.
- Lindholm, M., Eggertsson, O., Lovellus, N., Raspopov, O., Shumilov, O. & Laanelaid, A. 2001. Growth indices of North European Scots pine record the seasonal North Atlantic Oscillation. *Boreal Environment Research*, **6**, 275–284.
- Linville, S. U., Breitwisch, R. & Schilling, A. J. 1998. Plumage brightness as an indicator of parental care in northern cardinals. *Animal Behaviour*, **55**, 119–127.
- McNeil, K., Newman, I. & Kelly, F. J. 1996. *Testing Research Hypotheses with the General Linear Model*. Carbondale and Edwardsville, Illinois: Southern Illinois University Press.
- Mänd, R., Tilgar, V. & Møller, A. P. 2005. Negative relationship between plumage colour and breeding output in female great tits, *Parus major*. *Evolutionary Ecology Research*, **7**, 1013–1023.
- Martin, T. E. & Badyaev, A. V. 1996. Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. *Evolution*, **50**, 2454–2460.
- Mauck, R. A., Huntington, C. E. & Grubb, T. C. 2004. Age-specific reproductive success: evidence for the selection hypothesis. *Evolution*, **58**, 880–885.
- Michl, G., Török, J., Griffith, S. C. & Sheldon, B. C. 2002. Experimental analysis of sperm competition mechanisms in a wild bird population. *Proceedings of the National Academy of Sciences, U.S.A.* **99**, 5466–5470.
- Møller, A. P. 1989. Viability costs of male tail ornaments in a swallow. *Nature*, **339**, 132–135.
- Møller, A. P. 1991. Sexual selection in the monogamous barn swallow (*Hirundo rustica*). I. Determinants of tail ornament size. *Evolution*, **45**, 1823–1836.
- Møller, A. P. 1993. Sexual selection in the barn swallow *Hirundo rustica* III. Female tail ornaments. *Evolution*, **47**, 417–431.
- Møller, A. P. & Szép, T. 2005. Rapid evolutionary change in a secondary sexual character linked to climatic change. *Journal of Evolutionary Biology*, **18**, 481–495.
- Mougeot, F., Redpath, S. M. & Leckie, F. 2005. Ultraviolet reflectance of male and female red grouse, *Lagopus lagopus scoticus*: sexual ornaments reflect nematode parasite intensity. *Journal of Avian Biology*, **36**, 203–209.
- Muma, K. E. & Weatherhead, P. J. 1989. Male traits expressed in females: direct or indirect sexual selection? *Behavioral Ecology and Sociobiology*, **25**, 23–31.
- Nordeide, J. T., Rudolfson, G. & Egeland, E. S. 2006. Ornaments or offspring? Female sticklebacks (*Gasterosteus aculeatus* L.) trade off carotenoids between spines and eggs. *Journal of Evolutionary Biology*, **19**, 431–439.
- Omland, K. E. 1997. Examining two standard assumptions of ancestral reconstructions: repeated loss of dichromatism in dabbling ducks (Anatini). *Evolution*, **51**, 1636–1646.
- Orell, M. & Belda, E. J. 2002. Delayed cost of reproduction and senescence in the willow tit *Parus montanus*. *Journal of Animal Ecology*, **71**, 55–64.
- Palokangas, P., Korpimäki, E., Hakkarainen, H., Huhta, E., Tolonen, P. & Alatalo, R. V. 1994. Female kestrels gain reproductive success by choosing more ornamented males. *Animal Behaviour*, **47**, 443–448.
- Parker, T. H. & Garant, D. 2004. Quantitative genetics of sexually dimorphic traits and capture of genetic variance by a sexually selected condition-dependent ornament in red junglefowl (*Gallus gallus*). *Journal of Evolutionary Biology*, **17**, 1277–1285.
- Pärt, T. & Gustafsson, L. 1989. Breeding dispersal in the collared flycatcher (*Ficedula albicollis*): possible causes and reproductive consequences. *Journal of Animal Ecology*, **58**, 305–320.
- Pärt, T. & Qvarnström, A. 1997. Badge size in collared flycatchers predicts outcome of male competition over territories. *Animal Behaviour*, **54**, 893–899.
- Pettifor, R. A., Perrins, C. M. & McCleery, R. H. 2001. The individual optimization of fitness: variation in reproductive output, including clutch size, mean nestling mass and offspring recruitment, in manipulated broods of great tits *Parus major*. *Journal of Animal Ecology*, **70**, 62–79.
- Piersma, T., Mendes, L., Hennekens, J., Ratiarison, S., Groenewold, S. & Jukema, G. 2001. Breeding plumage honestly signals likelihood of tapeworm infestation in females of a long-distance migrating shorebird, the bar-tailed godwit. *Zoology*, **104**, 41–48.
- Postma, E. & van Noordwijk, A. J. 2005. Gene flow maintains a large genetic difference in clutch size at a small spatial scale. *Nature*, **433**, 65–68.
- Potti, J. & Merino, S. 1996. Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: implications for sexual selection. *Proceedings of the Royal Society of London, Series B*, **263**, 1199–1204.
- Potti, J. & Montalvo, S. 1991. Male arrival and female mate choice in pied flycatchers *Ficedula hypoleuca* in central Spain. *Ornis Scandinavica*, **22**, 45–54.
- Price, D. K. 1996. Sexual selection, selection load and quantitative genetics of zebra finch bill colour. *Proceedings of the Royal Society of London, Series B*, **263**, 217–221.
- Price, D. K. & Burley, N. T. 1994. Constraints on the evolution of attractive traits: selection in male and female zebra finches. *American Naturalist*, **144**, 908–934.
- Proulx, S. R., Day, T. & Rowe, L. 2002. Older males signal more reliably. *Proceedings of the Royal Society of London, Series B*, **269**, 2291–2299.
- Radesäter, T. & Jakobsson, S. 1989. Song rate correlations of replacement territorial willow warblers *Phylloscopus trochilus*. *Ornis Scandinavica*, **20**, 71–73.
- Regosin, J. V. & Pruett-Jones, S. 2001. Sexual selection and tail-length dimorphism in scissor-tailed flycatchers. *Auk*, **118**, 167–175.



- Roff, D. A. 2001. *Life-history Evolution*. Sunderland, Massachusetts: Sinauer.
- Rohde, P. A., Johnsen, A. & Lifjeld, J. T. 1999. Female plumage coloration in the bluethroat: no evidence for an indicator of maternal quality. *Condor*, **101**, 96–104.
- Roulin, A. 1999. Nonrandom pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait. *Behavioral Ecology*, **10**, 688–695.
- Roulin, A. & Dijkstra, C. 2003. Genetic and environmental components of variation in eumelanin and pheomelanin sex-traits in the barn owl. *Heredity*, **90**, 359–364.
- Safran, R. J. & McGraw, K. J. 2004. Plumage coloration, not length or symmetry of tail streamers, is a sexually selected trait in North-American barn swallows. *Behavioral Ecology*, **15**, 455–461.
- Senar, J. C. 1999. Plumage colouration as a signal of social status. In: *Proceedings of the 22nd International Ornithological Congress* (Ed. by N. J. Adams & R. H. Slotow), pp. 1669–1686. Johannesburg: BirdLife South Africa.
- Sheldon, B. C. & Ellegren, H. 1999. Sexual selection resulting from extrapair paternity in collared flycatchers. *Animal Behaviour*, **57**, 285–298.
- Siefferman, L. & Hill, G. E. 2005a. Evidence for sexual selection on structural plumage coloration in female eastern bluebirds (*Sialia sialis*). *Evolution*, **59**, 1819–1828.
- Siefferman, L. & Hill, G. E. 2005b. Male eastern bluebirds trade future ornamentation for current reproductive investment. *Biology Letters*, **1**, 208–211.
- Stenseth, N. C., Ottersen, G., Hurrell, J. W., Myrsetrud, A., Lima, M., Chan, K.-S., Yoccoz, N. G. & Ådlandsvik, B. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London, Series B*, **270**, 2087–2096.
- Svensson, L. 1992. *Identification Guide to European Passerines*. Stockholm: Svensson.
- Török, J. & Tóth, L. 1988. Density dependence in reproduction of the collared flycatcher (*Ficedula albicollis*) at high population levels. *Journal of Animal Ecology*, **57**, 251–258.
- Török, J., Hegyi, G. & Garamszegi, L. Z. 2003. Depigmented wing patch size is a condition-dependent indicator of viability in male collared flycatchers. *Behavioral Ecology*, **14**, 382–388.
- Török, J., Hegyi, G., Tóth, L. & Könczey, R. 2004. Unpredictable food supply modifies costs of reproduction and hampers individual optimization. *Oecologia*, **141**, 432–443.
- Turner, A. K. 1982. Timing of laying by swallows (*Hirundo rustica*) and sand martins (*Riparia riparia*). *Journal of Animal Ecology*, **51**, 29–46.
- Velando, A., Lessells, C. M. & Marquez, J. C. 2001. The function of female and male ornaments in the Inca tern: evidence for links between ornament expression and both adult condition and reproductive performance. *Journal of Avian Biology*, **32**, 311–318.
- Wiebe, K. L. & Martin, K. 1998. Age-specific patterns of reproduction in white-tailed and willow ptarmigan *Lagopus leucurus* and *L. lagopus*. *Ibis*, **140**, 14–24.
- Wiens, J. J. 1999. Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards. *Proceedings of the Royal Society of London, Series B*, **266**, 1529–1535.
- Wiley, C., Bengtson, J. M., Svedin, N. & Qvarnström, A. 2005. Hybridization costs of delayed maturation of secondary sexual traits in the collared flycatcher. *Evolution*, **59**, 2711–2716.
- Williams, T. D. & Christians, J. K. 2003. Experimental dissociation of the effects of diet, age and breeding experience on primary reproductive effort in zebra finches *Taeniopygia guttata*. *Journal of Avian Biology*, **34**, 379–386.
- Wolf, W. L., Casto, J. M., Nolan, V. & Ketterson, E. D. 2004. Female ornamentation and male mate choice in dark-eyed juncos. *Animal Behaviour*, **67**, 93–102.
- Wooller, R. D., Bradley, J. S., Skira, I. J. & Serventy, D. L. 1990. Reproductive success of short-tailed shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. *Journal of Animal Ecology*, **59**, 161–170.
- Zveryaev, I. I. 2004. Seasonality in precipitation variability over Europe. *Journal of Geophysical Research: Atmospheres*, **109** (D5).