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

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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.

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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). 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. Download English Version:

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