

Depigmented wing patch size is a condition-dependent indicator of viability in male collared flycatchers

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Honesty of sexual advertisement is thought to be the result of signalling costs. Because production costs of depigmented plumage patches are probably very low, their role as honest signals of individual quality has been questioned. Costs of bearing these traits, however, should also be taken into account. Studies on proximate determination and possible information content of white badges are very rare. We investigated repeatability, *sensu lato* heritability, and condition- and age-dependence of white wing patch size, a male display trait in a population of collared flycatchers (*Ficedula albicollis*), based on 4 years of data. By comparing relationships between age and wing patch size (1) within individuals among years versus (2) among individuals within years, we could address the viability indicator value of the trait. Wing patch size approximately doubled at the transition from subadult to adult plumage, and its change was significantly related to body condition the previous season. Repeatability and heritability values suggest that the trait is informative already in subadult plumage, and that genetic and early environmental effects are important in its determination, the latter only during the first year of life. Thus, wing patch size can act as a condition-dependent signal of genetic quality. Indeed, discrepancy between results from the horizontal and vertical age-dependence approaches shows that the trait was positively related to expected lifespan. After examining several alternative explanations, we conclude that wing patch size indicates genetically based viability. This is the first study to demonstrate a good genes viability benefit conferred by a depigmented plumage patch. *Key words*: condition-dependence, good genes signaling, heritability, plumage coloration, repeatability, viability. [*Behav Ecol* 14:382–388 (2003)]

Mate choice in relation to plumage traits is a general phenomenon in birds, but the advantages supporting time- and energy-consuming choosiness seem very variable (Andersson, 1994). These can be categorized as material or genetic. Material benefits are manifested during the current breeding season, and include, for example, territory quality (Radesäter and Jakobsson, 1989), and male parental quality (Buchanan and Catchpole, 2000; Sætre et al., 1995). The two main categories of genetic benefits are future attractiveness (Pomiankowski and Møller, 1995) and improved viability (Jennions et al., 2001; Møller and Alatalo, 1999) of offspring from a more ornamented father.

Metabolic origin of a signal may be important in determining its information content. For example, melanin-based plumage colors are thought to be less likely indicators of individual quality than those containing carotenoid pigments (Hill and Brawner, 1998; but see Slagsvold and Lifjeld, 1992). Recently, variability, role, and informativity of ultraviolet structural colours as mate-choice signals have been the subject of several investigations (see Andersson et al., 1998; Bennett et al., 1997; Keyser and Hill, 1999). White patches on a dark background have rarely been studied so far in this context (Höglund et al., 1990; Kose and Møller, 1999; for examples with social signalling function, see Senar, 1999). The benefit gained from choosing these traits is not straightforward, as their value as honest signals must stem from maintenance (instead of production) costs, the impor-

tance of which is not widely accepted (Badyaev and Hill, 2000; Hill and Brawner, 1998; but see Berglund et al., 1996; Qvarnström and Forsgren, 1998).

Multiple signaling seems widespread in birds (Hagelin, 2002; Møller et al., 1998; Zuk et al., 1992). Its study frequently involves traits that are very different in terms of flexibility and likely information value (see Hill et al., 1999; Møller et al., 1998). A contrasting recent approach is to consider individual traits as composite signals with potentially multiple lines of information content (Badyaev et al., 2001; Møller and Petrie, 2002). Somewhere between these two extremes lies the investigation of disjunct traits that have a similar metabolic origin, for example, multiple white plumage patches on different body parts (Sheldon and Ellegren, 1999). An interesting question is whether these signal different facets of individual quality, or convey the same message more reliably (Møller and Pomiankowski, 1993; Johnstone, 1996). It cannot be answered until one demonstrates that both traits in question are sexually selected, and analyzes their proximate determination in sufficient detail.

Forehead patch size of male collared flycatchers (*Ficedula albicollis*) is the single thoroughly studied depigmented plumage signal so far. In a Swedish population, the trait has been shown to be condition-dependent, reflecting previous reproductive effort (Gustafsson et al., 1995), and sexually selected in terms of male-male competition for nest-boxes (Pärt and Qvarnström, 1997), female choice at settlement (Qvarnström et al., 2000), polygyny (Gustafsson et al., 1995), and extra-pair paternity (Sheldon and Ellegren, 1999; Sheldon et al., 1997). Data from other localities show that phenotypic variation, determination, and role of this same trait is different in different populations of this and the sibling species *F. hypoleuca* (Dale et al., 1999; Hegyi et al., 2002).

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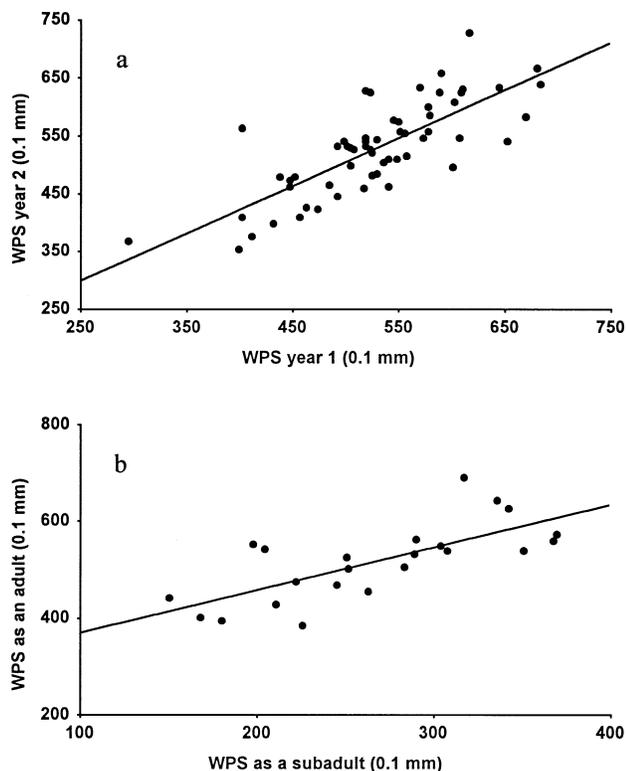


Figure 1
Repeatability of wing patch size (WPS) within adult collared flycatcher males (a) and at the transition from subadult to adult plumage (b).

The white wing bar of collared flycatcher males is displayed both during male-male contests (personal observations) and courtship flights (Gustafsson et al., 1994), and it has been shown to be sexually selected in a Swedish population (Sheldon and Ellegren, 1999). In this paper we examined proximate determination of this trait in a Central-European population based on four years of data. We also investigated the relationship between wing patch size (WPS) and age by two methods: among age categories within years and within individuals between consecutive years. A comparison of the detailed results from these two analyses also has the potential to reveal correlation of attractiveness with expected survivorship at a certain age (Cam and Monnart, 2000). This allows us to address the viability indicator value of the trait.

METHODS

Collared flycatchers are long-distance migratory, hole-nesting, insectivorous passerines (family Muscicapidae). This species is suited to long-term studies as its breeding site fidelity is very high (Gustafsson, 1989). The ornamental breeding plumage of males is black and white, with prominent white forehead and wing patches and collar. It is acquired during the complete moult at the winter quarters in South Africa (Svensson, 1992). Breeding phenology of the species is described in detail by Gustafsson (1989).

Our nest-box-breeding population of collared flycatchers in Pilis Mountains, Hungary, was established in the early 1980s. The study plots are parts of a continuous, unmanaged, oak-dominated woodland, a strictly protected area of Duna-Ipoly National Park since 1997. The total number of nest-

boxes is now approximately 600. For a more detailed description of the study site see Török and Tóth (1988).

Males were captured in the nest-box either shortly after their arrival or when feeding young. Tarsus length and body mass were measured with a dial caliper (nearest 0.1 mm) and a Pesola spring balance (nearest 0.1 g), respectively. The use of tarsus length as an estimate of body size in this species has been justified by a large number of studies (see Gustafsson et al., 1995; Qvarnström, 1999). Tarsus length and body mass were year-standardized before entering them to the analyses. In accordance with recent recommendations (García-Berthou, 2001), we estimated body condition by entering tarsus length as a covariate into the analyses of body mass. As width of the wing patch changes continuously with wing movements, we recorded (by caliper, nearest 0.1 mm) the sum of lengths of white from the tip of primary coverts on the outer web of fourth to eighth primaries on the right wing. There is no directional and very small fluctuating asymmetry (data not shown). The values on the different primaries are very highly positively correlated (all $p < .001$). Estimated measurement repeatability of WPS based on within-season repeated measurement of 11 adult males is 0.830 ± 0.072 SE. As WPS is bimodally distributed, we separated subadult and adult males for the correlative tests. To avoid pseudoreplication, when necessary, each male was represented by his first measured WPS or his first pair of seasons with WPS measured in the among- and within-individual analyses, respectively.

Male ages are accurate for recruits or males ringed in subadult plumage ($n = 195$). Based on a large set of offspring recruitment data, we assigned an age of 2 years at first encounter to males ringed in adult plumage ($n = 135$). As omitting males with age that had only been estimated did not affect any of our conclusions on age-dependence, we present results based on all individuals with measured WPS. Between-individual age category 4 comprises all males older than 3 years.

We estimated heritability as twice the slope of a son/father regression. WPS within individuals increased after the second year to an average 2.01 ± 0.38 times its original size ($n = 23$). To allow for this change in heritability calculations, we fitted a two-way ANCOVA with father and son binary ages as factors, son WPS as dependent variable, and father WPS as a covariate. Owing to the small number of subadult fathers ($n = 4$), it would be meaningless to report heritability values for the two father ages separately. There was no such problem with son age, so we could compare heritability estimates for subadult versus adult sons. This method provides information on short-term early environmental (e.g., maternal) effects biasing son-father similarity. Values of recruits originating from the same father were averaged for the heritability calculations irrespective of whether they had come from the same or from different broods. In cases of one adult and one subadult recruit from the same father, the subadult was used. All probabilities are two-tailed. We used Statistica 4.5 (StatSoft, Inc., Tulsa, Oklahoma, 1993) throughout. Data are presented as mean \pm SE unless otherwise noted.

RESULTS

Proximate determination of WPS

The repeatability of WPS within adults is large (Figure 1a; $b = 0.825 \pm 0.089$, $F_{1,57} = 86.650$, $r^2 = .603$, $p < .001$). The heritability estimate based on the measured recruits with father of known WPS within this period is different for subadult versus adult recruits, although the difference is not

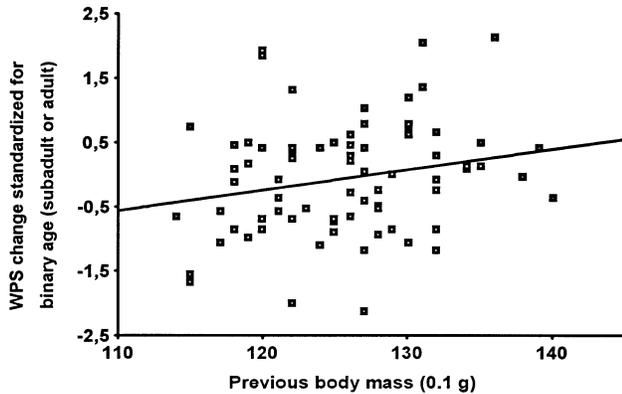


Figure 2
Between-year changes of wing patch size (WPS) in collared flycatcher males as predicted by body mass in the first of the two seasons.

significant with these sample sizes (two-way ANCOVA with father and son binary ages as factors, one-way test of parallelism; $n = 29$, $F_{1,23} = 1.510$, $p = .232$). The similarity is very high in subadults ($n = 15$, $b = 0.545 \pm 0.142$, $r^2 = .551$, $F_{1,12} = 14.715$, $p = .002$) but lower in adults ($n = 14$, $b = 0.263 \pm 0.183$, $r^2 = .158$, $F_{1,11} = 2.069$, $p = .178$). Heritability estimates based on the two groups are 1.090 and 0.526, respectively. Nevertheless, the correlation between WPS in subadult and adult plumage within individuals is high (Figure 1b; $b = 0.879 \pm 0.183$, $r^2 = .523$, $F_{1,21} = 22.987$, $p < .001$). WPS was not related to body size (tarsus length, ANCOVA with binary age [subadult or adult] as a factor; test of parallelism: $F_{1,304} = 1.638$, $p = 0.202$; within-cell regression: $r^2 = .001$, $F_{1,305} = 0.344$, $p = .558$) or current body condition (ANCOVA with body mass and tarsus length as covariates; mass: $\beta = 0.032$, $t_{295} = 0.525$, $p = .600$; parallelism: $F_{2,293} = 1.791$, $p = .169$). Body condition during the first of two consecutive seasons significantly predicted change in WPS between these seasons (Figure 2; ANCOVA as above; mass: $\beta = 0.277$, $t_{71} = 2.187$, $p = .032$; parallelism: $F_{2,69} = 0.570$, $p = .568$). WPS was positively related to area of the white forehead patch (ANCOVA; $F_{1,271} = 6.053$, $p = .015$; parallelism: $F_{1,270} = 0.001$, $p = .974$).

Age and WPS among individuals

A two-way ANOVA, with four-level age category and year as factors, revealed a significant effect of age category (Figure 3a; $F_{3,314} = 199.407$, $p < .001$) but no influence of year ($F_{3,314} = 1.655$, $p = .177$) or interaction ($F_{3,314} = 0.935$, $p = .495$). For age, all post hoc comparisons (least significant difference tests) are significant except between categories 2 and 3. Rank order of age categories is very consistent among years: mean WPS in categories 1 and 4 are the smallest and the largest, respectively, in all 4 years (Table 1).

Among-individual improvement in a character can result from late breeding by individuals with high trait values. In our case, however, WPS was not taken for all measured males in 1998 and 1999. Nineteen out of the 24 males in the minimum age category 4 had already been captured earlier as 1- ($n = 7$), 2- ($n = 11$) or 3-year-olds ($n = 1$). If we omit the remaining five individuals (real late first measurements), the results remain unchanged (ANOVA for minimum age; categories 2-3-4: $F_{2,218} = 5.077$, $p = .007$; post-hoc test for categories 2-3: $p = .265$, categories 2-4: $p = .005$, categories 3-4: $p = .003$).

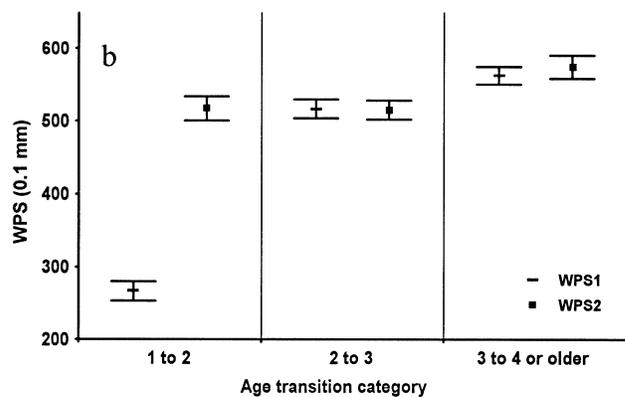
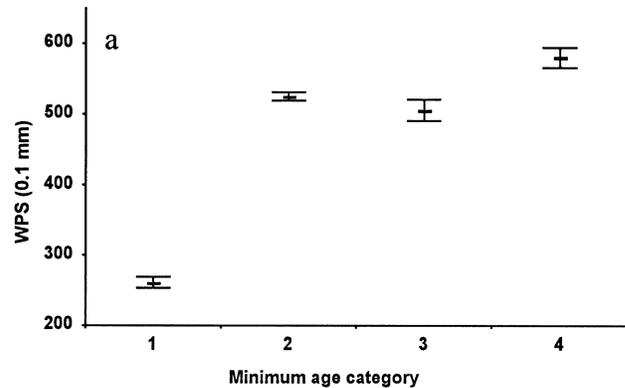


Figure 3
Male wing patch size (WPS) and age in collared flycatchers among individuals within years (a) and within individuals between consecutive seasons (b).

Age and WPS within individuals

As no measured subadult male returned from 1998, we conducted separate repeated-measures ANOVA-s for three age transitions (1 to 2, 2 to 3, and after 3 years of age) with year as a factor. There was a significant increase from 1 to 2 years of age, but no consistent change later on in adult plumage (Figure 3b; Table 2). Neither year-effect nor interaction was observed (Table 2). Small number of data ($n = 15$) in the oldest age transition category is unlikely to have affected these results, as the between-individual pattern among old males remains significant in this reduced dataset (second measurements; $F_{2,76} = 3.449$, $p = .037$; post-hoc tests between categories 2-3: $p = .916$, categories 2-4: $p = .030$, categories 3-4: $p = .014$; see difference between means in the middle and the right block of Figure 3b). Furthermore, in contrast to the extreme among-year consistency of the between-individual differences, the mean within-individual change in the third age transition category was positive in 1998–1999, negative in 1999–2000, and close to zero in 2000–2001 (data not shown).

DISCUSSION

WPS of males in our collared flycatcher population is flexible to some degree. Its change between seasons was significantly affected by previous body condition (Figure 2). It also showed, however, very high repeatability (Figure 1), and high heritability, which indicate a large additive genetic and/or

Table 1
Wing patch sizes of collared flycatcher males: year-wise means of the four age categories

Year	Minimum age category	Mean (mm)	SD	Valid <i>N</i>
1998	1	29.10	9.80	8
1998	2	51.80	8.82	29
1998	3	55.12	9.97	4
1998	4	60.41	2.91	3
1999	1	28.44	7.66	31
1999	2	55.04	7.01	51
1999	3	47.66	7.87	8
1999	4	59.01	7.22	11
2000	1	25.15	7.59	50
2000	2	52.30	8.07	42
2000	3	50.76	1.82	7
2000	4	58.33	9.34	6
2001	1	22.81	5.80	15
2001	2	50.72	7.97	57
2001	3	51.48	8.76	4
2001	4	52.88	3.23	4

early environmental influence. Father-offspring similarity was much more pronounced in subadult than in adult recruits. The heritability estimate based on adult recruits ($h^2 = 0.526$) is slightly lower than that of forehead patch size in this same population ($h^2 = 0.584$, $n = 124$; Hegyi et al., 2002), which is condition-independent and thus cannot be biased by early environment. This suggests that the father-son correlation of WPS is inflated by early environmental effects, but these are not important beyond one year of age. These results allow us to think about WPS as a potential condition-dependent signal of genetic quality (Rowe and Houle, 1996). The high correlation between WPS in subadult and adult plumage within individuals (Figure 1b), despite the approximately twofold difference in values, shows that relative signal value is likely to convey similar information in subadults and adults.

Difference between two age classes in a trait may be the result of either a systematic change within individuals, or a trait-related change between the two ages in the composition of the cohort (Forslund and Pärt, 1995). The latter can be of two types: entry of new individuals whose values of the trait do not match the population mean (Nol and Smith, 1987), or a disappearance of individuals that is not random with respect to the trait (Cam and Monnat, 2000). In our case, a comparison of results from the between- and within-individual approaches (Figure 3) reveals that the approximately twofold difference in WPS between second-year and older males is a result of a significant increase during transition from subadult to adult plumage. On the other hand, the significant difference between third- or fourth-year and older males remains unexplained by within-individual changes. One possible

reason for this pattern is delayed breeding by extremely large patched males (Forslund and Pärt, 1995). It seems especially straightforward as we used “first wing patch measurements” in the between-individual database. Age at first WPS record, however, has little to do with age at first breeding in our data set, and omitting real late breeders did not affect the results. Another reason would be a year-effect. There was no sign of year-effect on WPS within the 4 years of measurement. There was also no interaction between age and year in the among-individual ANOVA, and WPS of the fourth age category was larger than all others in all 4 years. This would require that positive year-effects had been present in at least four consecutive seasons before the study period, which is highly unlikely. The remaining explanation for the difference between horizontal and vertical results is selection (Cam and Monnat, 2000): Males who qualified for age category 4 had particularly large wing patches. A comparison of the wing patch of survivors and nonsurvivors in age categories 1 and 3 also supports this reasoning (Figure 4).

There is an ongoing debate on how plumage coloration can indicate individual quality. Some authors argue that metabolic costs are very important in this respect (Badyaev and Hill, 2000). From this point of view, carotenoid pigments are more likely candidates to form reliable signals of individual quality in birds than is melanin, as carotenoids come exclusively from the diet (Brush, 1990), and their occurrence is generally limiting (Linville and Breitwisch, 1997). Support for this view is equivocal. There is correlative and experimental evidence that melanin-based ornaments are not influenced by body condition in species who have condition-dependent carotenoid signals (Hill and Brawner, 1998; McGraw and Hill, 2000). In house sparrows, in contrast, black badge size reflects body condition (Griffith, 2000), but the genetic determination of the trait seems minimal (Griffith et al., 1999). In Scandinavian pied flycatchers, melanin-based plumage hue is a condition-dependent indicator of male parental quality (Sætre et al., 1995; Slagsvold and Lifjeld, 1992). Moreover, Swedish collared flycatchers, in contrast to our population (Hegyi et al., 2002), adjust heritable white forehead patch size to condition (Gustafsson et al., 1995; Qvarnström, 1999).

If judged from its production costs, WPS of a male collared flycatcher would be especially unlikely to convey information on the quality of its bearer, as it is not only melanin-based but white on a black background, which means that the larger it is, the less melanin it requires. Indeed, the most straightforward explanation for our results is that large wing patches are less costly than small ones. We cannot accept this view for several reasons.

On one hand, the cost of investing melanin to some additional square millimeters of feathers is probably close to zero (Badyaev and Hill, 2000). On the other hand, recent experiments have shown that maintenance costs of more white in the plumage are far from negligible. Male collared flycatchers whose forehead patch had been artificially

Table 2
Age-related changes of wing patch size in male collared flycatchers: repeated-measures ANOVAs with year as a factor

Age transition	Repeated-measures factor							Year		Interaction	
	Mean 1 (mm)	SD 1	Mean 2 (mm)	SD 2	<i>n</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
1–2	26.64	6.48	51.70	7.87	23	417.02	0.001	0.03	0.853	0.67	0.422
2–3	51.63	8.24	51.48	8.22	41	0.71	0.406	0.21	0.809	1.68	0.199
Older	56.23	4.70	57.42	6.22	15	0.19	0.667	1.44	0.275	32.6	0.074

enlarged early in the breeding season developed higher levels of Haematozoa (Gustafsson et al., 1994) and showed a lower offspring feeding activity (Qvarnström, 1997) than control males. Males of the single-brooded, long-distance migratory *Ficedula* species cannot perform extra-pair copulations in the nestling rearing period, as their gonads begin to regress after their mates laid their first egg (Birkhead et al., 1997). Thus, the reason for the above results is probably a deterioration of body condition owing to increased male-male aggression in the enlarged category (Qvarnström, 1997). The wing patch is likely to elicit the same or an even higher level of aggression from other males than is the forehead badge, as it is larger, and very conspicuous not only during territorial conflicts but also in regular flight (Jablonski, 1996).

Furthermore, melanin structurally strengthens feathers, which frequently suffer from an increased wear (Bonsler, 1995) and a higher probability of breakage (Kose and Møller, 1999) in white areas. Chewing lice may also preferentially harm white areas (Kose and Møller, 1999). A white patch on the primaries is thus likely to interfere with flying proficiency.

Finally, and perhaps most importantly, the generally accepted evolutionary explanation for condition-dependence of mate-choice signals is their costliness (Rowe and Houle, 1996). From this point of view, our finding that within-individual change in WPS was significantly positively related to body condition (Figure 2) provides evidence that net cost of the trait depends positively rather than negatively on its size. In sum, as painting is likely to affect the functional structure of flight feathers, experimental demonstration of maintenance costs of WPS would require phenotypic engineering techniques yet to be developed, but available data strongly suggest that these costs exceed the minimal benefit of producing less melanin.

The relationship between WPS and survival is also unlikely to be the result of early environmental effects (Gil et al., 1999), because, as discussed above, these are apparently minimal after the second year of life. Another possibility is that improved survivorship is a consequence of, rather than reason for, large WPS. For example, repeated material advantages for large-patched males might promote their survival. However, these external environmental effects should have also caused a monotonous within-individual improvement in the condition-dependent WPS with advancing age (see Pärt, 2001). This was clearly not the case: After reaching 2 years of age, within-individual changes were variable, but with no overall direction, irrespective of year. A predator-deterrent function of large wing patches is very unlikely, as (1) even the evidence that black-and-white male (in contrast to greyish female) plumage reduces predation risk (Götmark, 1995) has been questioned (Slagsvold et al., 1995), and (2) it is highly unlikely that a generalist predator uses some square millimeters of patch size difference to decide whether attack or not, as its sensory system is unlikely to be tuned to detect small difference in the relevant (i.e., quality-indicator) cues on the plumage of each of its several prey species. This adaptation to quick quality assessment would be further complicated by the fact that there may be difference among populations of a single prey with respect to information content of plumage signals (Badyaev et al., 2001; Hegyi et al., 2002).

The remaining explanation for the improved longevity of males with large wing patches is a genetic quality effect. The co-occurrence of large heritability, repeatability, and condition-dependence found in this study characterizes good-genes signals (Rowe and Houle, 1996). This means that genes for conspicuousness are in fact genes for consistently superior body condition, one possible effect of which is a higher probability of survival. Our heritability data show that early environmental effects may not confound genetic effects

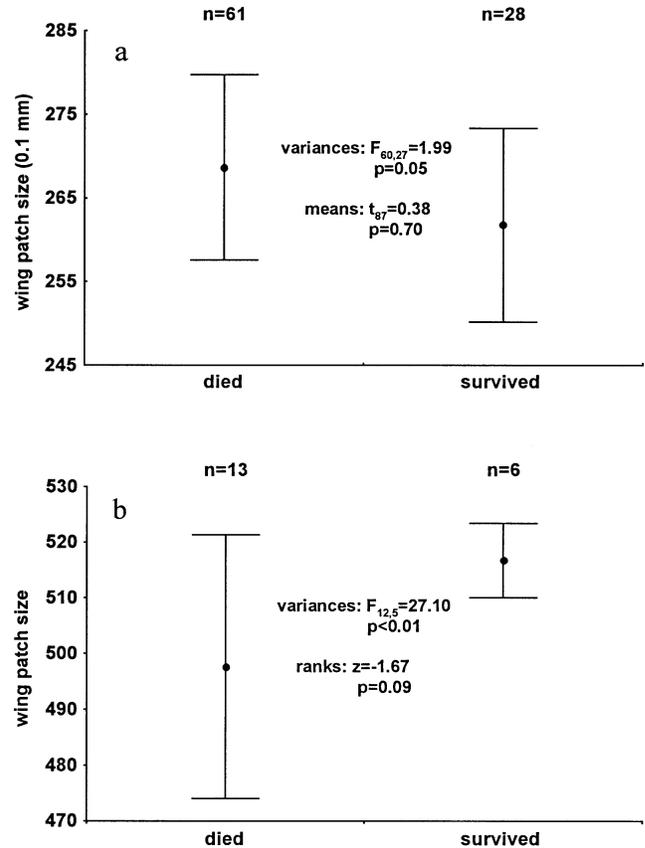


Figure 4

Male wing patch size in relation to survival to the next breeding season among 1-year old (a) and 3-year old (b) collared flycatcher males in 1998–2000.

beyond the first year of life. In light of this, the very large between-season repeatability of male body condition previously demonstrated for this population (0.802 ± 0.055 , $n = 164$; Hegyi et al., 2002) suggests a large proportion of additive genetic determination. Body condition in the previous breeding season explained a significant proportion of variance in subsequent WPS (Figure 2) despite the fact that the ornament is developed during the winter moult (Svensson, 1992). We therefore conclude that repeatability and heritability of WPS is a genetic effect through body condition (Rowe and Houle, 1996). This implies that WPS is a good genes indicator of viability in our population. To our knowledge, our results are the first to suggest that white plumage signals can indicate genetically based viability.

The survival advantage of large-patched males appeared only beyond the age of 3 years. This surprising pattern cannot be attributed to a partially incorrect assignment of age, because the results were the same when we used only males with an exactly known age (ringed as nestling or subadult). Another possible explanation is higher reproductive effort of older individuals and a resultant additional selection pressure. For example, it is known that reproductive effort of collared flycatcher females increases with age (Pärt et al., 1992). Qvarnström (1999) examined, among else, the effect of maternal age on condition-dependent badge size of recruited offspring. She showed that female parental quality of second- and third-year birds was similar, but that of individuals older than these was much higher. This late investment in reproduction exerts an increased selection pressure for self-maintenance efficiency. In other words, only the best females

can survive it. If some reproductive effort component of males in our population analogously increases with advancing age, then it is also expected to exaggerate the effect of quality differences among particularly old males, and may explain our results.

These are also among the first results to indicate that choosing plumage signals of the same metabolic basis within the same population may confer qualitatively different benefits to the choosy sex (Badyaev et al., 2001). Area of the white forehead patch is sexually selected in our population (Michl et al., 2002), but despite being positively related to WPS, and in contrast to the Swedish population (Gustafsson et al., 1995), it is largely independent of age and unrelated to body condition (Hegyí et al., 2002). It also shows slight negative relationship to survival probability and no relationship to lifespan (Hegyí et al., 2002). The reason for this difference in proximate determination between forehead and wing ornaments may be that wear of depigmented areas on the primaries is likely to have a negative impact on flight performance, but forehead patch abrasion is probably unimportant to fitness components other than sexual selection. Given the widespread occurrence of white wing patches among birds (Price and Pavelka, 1996), some of which plays (Jablonski and Matyjasiak, 2002) or is likely to play (Ruusila et al., 2001) a within-species signaling role, their maintenance costs deserve further investigation.

To summarize, we have shown that white WPS of male collared flycatchers in our population is condition-dependent, highly repeatable, and heritable, and it consistently predicts adult survivorship beyond the age of three years. The trait seems a particularly interesting case of good genes signalling, as its production costs are, to the best of our knowledge, minimal. Costs of bearing large white patches on the primaries probably include increased male-male aggression and impaired resistance to feather abrasion and breakage. The importance of maintenance costs in ensuring honesty of plumage ornamentation, and the generality of the role of depigmented plumage ornaments as indicators of genetic quality are fruitful areas for future research.

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