

The roles of ecological factors and sexual selection in the evolution of white wing patches in ducks

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Most studies of the evolution of sexual ornamentation have dealt with plumage attributes. White plumage patches are widespread in birds, the disproportionate role of wearing costs makes their evolutionary trajectories unique, and their visual assessment is less biased than that of other color categories. Still, comparative studies of white patches are very rare. We examined the evolution of white wing patches in ducks (Anatinae), assessing both sex-specific trait expression and dichromatism. Habitat openness, nest site (cavity or open), or the length of the incubation period did not predict white patch expression. Patch size on the wing coverts of females increased with parental care contribution by males. Covert patch size relative to the wing surface was positively related to body size in males, suggesting a role in sexual competition. White wing patch expression was unrelated to the frequency of social mate change or testis size, a measure of general sperm competition intensity. However, covert patch size in both sexes showed strong negative correlation with the phallus length of males, an indicator of the prevalence of forced copulations. Further studies are needed to clarify the role of flight feather patches and the factors that limit the exaggeration of white wing patches in this and other groups. *Key words*: Anatinae, forced copulation, intrasexual competition, parental care, predation, social mating system, white plumage ornament. [*Behav Ecol* 19:1208–1216 (2008)]

Sexual selection is generally recognized as a potent force, shaping evolution from individual morphological traits (Andersson 1994) to adaptation to the prevailing environment (Hoekstra et al. 2001) as well as patterns of speciation (Boughman 2001) and extinction (Doherty et al. 2001). One of the most prominent features of sexual selection is the production of exaggerated ornamental traits used in signaling contexts (Darwin 1871). Comparative studies have repeatedly examined the distribution of ornamentation above the species level, by either using ornamentation as a surrogate of sexual selection intensity or trying to explain the phylogenetic distribution of ornamentation with objective measures of ecology and sexual selection. The largest number of studies dealt with plumage colors in birds (Hill and McGraw 2006).

Distinct white plumage patches are present in many species of birds (Price and Pavelka 1996). However, the role of white patches in sexual selection and their information content have been examined relatively rarely (Höglund et al. 1990; Kose et al. 1999; McGlothlin et al. 2005; Bókonyi et al. 2006; Hanssen et al. 2006), perhaps with the exception of Old world flycatchers (reviewed in Garant et al. 2004; Hegyi et al. 2006). White patches are special in at least 2 respects. First, they involve the lack of melanin in feathers, and their color is produced by incoherent light scattering which does not assume any structural adaptation in the feather (Prum 2006), so their production costs should be low. Accordingly, there is a major role for costs of wearing the trait, such as predation costs (Dale and Slagsvold 1996) and social costs (Qvarnström 1997). Second, melanin is important to the structural strength

of feathers (Bonser 1995). Consequently, wearing a white patch on the flight feathers involves the potentially significant additional cost of feather abrasion and breakage (Kose and Møller 1999). In spite of their unique characteristics, to the best of our knowledge, no comparative analysis has so far focused on the evolution of white plumage patches by sexual selection (for an ecological approach, see Brooke 1998).

The aim of the present study was to examine the phylogenetic distribution of white wing patches in ducks (Anatinae), in relation to several ecological factors and sexual selection measures. The nuptial plumage of ducks shows a bewildering variation of coloration (Madge and Burn 1987). Most of the ornamentation is absent during the period spent in eclipse plumage, but wing patterns are retained throughout the year and replaced only once a year (Pyle 2005). Human-scored overall plumage brightness in waterfowl has been shown to be related to social mating patterns and a variety of ecological characteristics (Scott and Clutton-Brock 1989). A subset of these variables was subsequently tested while controlling for phylogeny (Figueroa and Green 2000). Wing patterns are widely used in the displays of ducks, both in male–male and male–female contexts (e.g., Cramp 1997), although the only within-species study examining the role of the white wing patch in female mate choice did not find convincing evidence (Omeland 1996a, 1996b). Further tests are needed to reach any general conclusion. Finally, recent studies of ducks have suggested relationships between white wing patch size and female individual quality (Ruusila et al. 2001, Hanssen et al. 2006).

Although comparative studies of plumage coloration have so far gathered a very large body of evidence (Badyaev and Hill 2003), 3 recent findings have much rearranged the apparently coherent picture that previously emerged. First, high rates of evolutionary change in female ornamentation have been detected (Burns 1998; Amundsen 2000; Garamszegi et al. 2007),

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which suggests that sexual dimorphism in trait expression may not be a good measure of differences in sexual selection intensity among species (Irwin 1994; Wiens 2001). Second, biochemical studies have shown that using color to categorize plumage ornaments as carotenoid versus melanin based may not always provide reliable results (McGraw et al. 2004). It is therefore partly uncertain how we should interpret previous conclusions regarding the relative importance of carotenoid versus melanin ornamentation in sexual selection (Badyaev and Hill 2000; Badyaev et al. 2002; Bókonyi et al. 2003; Nadeau et al. 2007). Third, the importance of ultraviolet (UV) wavelengths in sexual signaling among birds has been increasingly recognized (Andersson et al. 1998; Johnsen et al. 2000). This may have profound implications for comparative studies of ornamentation, given that human-visible colors show variable association with UV reflectance (Eaton and Lanyon 2003), and patterns of dichromatism including the UV range are grossly inconsistent with categorization based on the human visual system (Eaton 2005).

These concerns give special importance to studies of white plumage patches. First, white patches are relatively easy to quantify objectively. This makes it a reasonable approach to assess ornamentation for the 2 sexes separately, without an exclusive focus on sexual dichromatism. Second, the biochemical and structural basis of white plumage patches is unambiguous, so it is certain that trait expression data from different taxa refer to the same phenomenon (Prum 2006). Finally, white plumage patches are monochromatic bright across the visual range of humans, and nearly all of them also have strong UV reflectance (Eaton and Lanyon 2003), so their assessment is not loaded with the magnitude of perceptual error observed with respect to other classes of colors.

Most of the predictors we shall use here are specifically relevant to our study system. For example, white patches on the wing are highly conspicuous, so they are expected to show evolutionary effects of visual communication and predation. This may affect the relationships of patch expression with habitat openness (Marchetti 1993), hole nesting (Scott and Clutton-Brock 1989), and the length of the incubation period in females (Martin and Badyaev 1996). The wearing costs of white patches, including predation and feather abrasion, may lead to an evolutionary correlation between patch expression and the distribution of parental care between the sexes (Kirkpatrick and Ryan 1991). Finally, in addition to classical measures of sexual selection such as social mating system and sperm competition (Scott and Clutton-Brock 1989; Figuerola and Green 2000; Dunn et al. 2001), we examine male intromittent organ size as a measure of the frequency of forced copulations (Coker et al. 2002). This behavior raises the issues of conspicuousness and possibly even visual communication, and it may therefore influence the evolution of white plumage traits.

METHODS

The expression of white patches

We used data only from the Anatinae subfamily (ducks). The analysis of Anserinae with respect to white wing patches did not seem fruitful because geese rarely have such traits, whereas the white overall color of swans makes it difficult to interpret white wing color in this group analogously to other species of the family. White wing patch expression was scored from paintings of flying birds in the global guide of Madge and Burn (1987). White patches on the coverts versus the flight feathers were scored separately. We expected different evolutionary patterns for the 2 areas because white patches on the flight feathers may be especially costly to wear (Kose and Møller 1999). Co-

vert patches received a score of 0 if absent and 1 or 2 if less or more than half the area of coverts, respectively, was white. Covert patches were scored on the upper surface of the wing. The distribution of flight feather patches was nested, so we devised a single scoring system for primaries and secondaries (0, no white patch; 1, distinct white trailing edge; 2, most of the visible area of some or all secondaries white; 3, most of the visible area of some or all secondaries and primaries white).

No qualitative sexual dichromatism was observed in flight feather patches, except for a single species, *Nettion coromandelianus*. However, males had higher covert patch expression than females in a number of species (difference of 1: $N = 7$; difference of 2: $N = 6$). Accordingly, our measures of patch expression were the following: flight feather patch score (both sexes, male in *N. coromandelianus*), male covert patch score, female covert patch score, covert patch dichromatism (1 if present, 0 if absent). Omitting *N. coromandelianus* from the analyses of flight feather patch scores yielded very similar results to those presented here. We note that although we will often refer to white patch expression as white patch size, this size is quantified relative to the wing surface, so it is not biased by body size for allometric reasons.

We assessed the objectivity of the patch size scoring in 2 ways. First, all species were rescored using one of several regional field guides (Falla et al. 1978; Pizzey and Doyle 1980; Coates et al. 1997; Heinzel et al. 1997; De la Peña and Rumboll 1998; MacKinnon and Phillipps 2000; National Geographic 2000; Souza 2002) as well as photographs published on the Internet. This second scoring was done by the authors, blind to the original scores of the species. Correlation between the 2 types of independent scores was strong (flight feather patch $r = 0.82$, $N = 101$, $P < 0.001$; male covert patch $r = 0.95$, $N = 101$, $P < 0.001$; female covert patch $r = 0.83$, $N = 101$, $P < 0.001$; covert patch dichromatism $\chi^2 = 30.63$, degrees of freedom [df] = 1, $P < 0.001$). Second, stuffed specimens of 41 species were located in the Natural History Museum of Budapest, Hungary. Two observers, unaware of the guidebook scores and working independently, quantified wing patch sizes on these specimens using the original criteria. Three specimens of both sexes were scored from most species. Median scores were then calculated between the observers and for each sex of each species. Although most specimens were preserved with folded wings and this makes it difficult to quantify wing patches, the median scores strongly correlated with our Madge and Burn (1987) guidebook scores (flight feather scores $r = 0.65$, $N = 41$, $P < 0.001$; male covert scores $r = 0.82$, $N = 33$, $P < 0.001$; female covert scores $r = 0.56$, $N = 29$, $P = 0.001$; dichromatism could not be compared because too few species dichromatic on the guidebook list could be scored in the museum). Based on the 2 validations, we can consider the guidebook scores as reliable representations of white wing patch expression patterns among species.

Explanatory variables

To quantify the importance of social mate choice, we used the binary mating system classification of Scott and Clutton-Brock (1989). Species with social pair-bonds longer than a year received a score of 1, whereas those pairing at least once a year were assigned a score of 2. Testis size data (residuals from a regression on body size) were obtained from Pitcher et al. (2005) and supplemented with additional data from Coker et al. (2002). We used residual testis masses from a linear regression on body size, where the line was fit to the whole supplemented data set. The length of the intromittent organ (in centimeter, hereafter referred to as phallus length) was measured by Coker et al. (2002) on formalin-preserved specimens. Data on male and female body mass were taken from

Figuerola and Green (2006) and log-transformed before analyses. In line with previous results (Coker et al. 2002), phallus length was unrelated to body mass (phylogenetic regression; $r = 0.064$, $P = 0.696$). We also calculated sexual size dimorphism (female mass per male mass). Data on habitat (1, open; 2, intermediate; 3, woodland or forest) were extracted from the descriptions of Del Hoyo et al. (1992). Nest sites (1 if cavity, 0 if open) were scored and incubation length defined as in Geffen and Yom-Tov (2001). Data on paternal care (1–3 with higher scores corresponding to less male care) were taken from Scott and Clutton-Brock (1989). The data set can be found in the online Supplementary material. Binary predictors were treated as discrete and all others as continuous traits in the analyses. The statistical reason behind treating variables with few possible states as continuous is that intermediate states are biologically meaningful, so different states are arbitrary points along a continuum (Sokal and Rohlf 1995). In addition, in an evolutionary context, a transition between 2 states of these variables is a nondiscrete evolutionary change. Therefore, the continuous treatment is generally

applied in comparative studies that are constrained to use nonquantitative data for a larger set of species (Harvey and Pagel 1991; Bennett and Owens 2002). As a result, one can show qualitatively that a given trait plays a role in the evolution of another but cannot assess its quantitative importance.

Statistical analyses

Data from different species cannot be regarded as independent, so analyses of comparative data should be conducted in a way that takes the variable degrees of relatedness into account. Our phylogeny of Anatinae was based on 2 genetically based subtrees of the group (Johnson and Sorenson 1999; Donne-Goussé et al. 2002). Polytomies were resolved and groups or species missing from these trees were added based on the morphological phylogeny of Livezey (1997; also see Figuerola and Green 2000; Geffen and Yom-Tov 2001). In 2 cases without appropriate information, we randomly deleted one species to remove a polytomy at a terminal node. Our final tree including 101 species is shown in Figure 1. Because

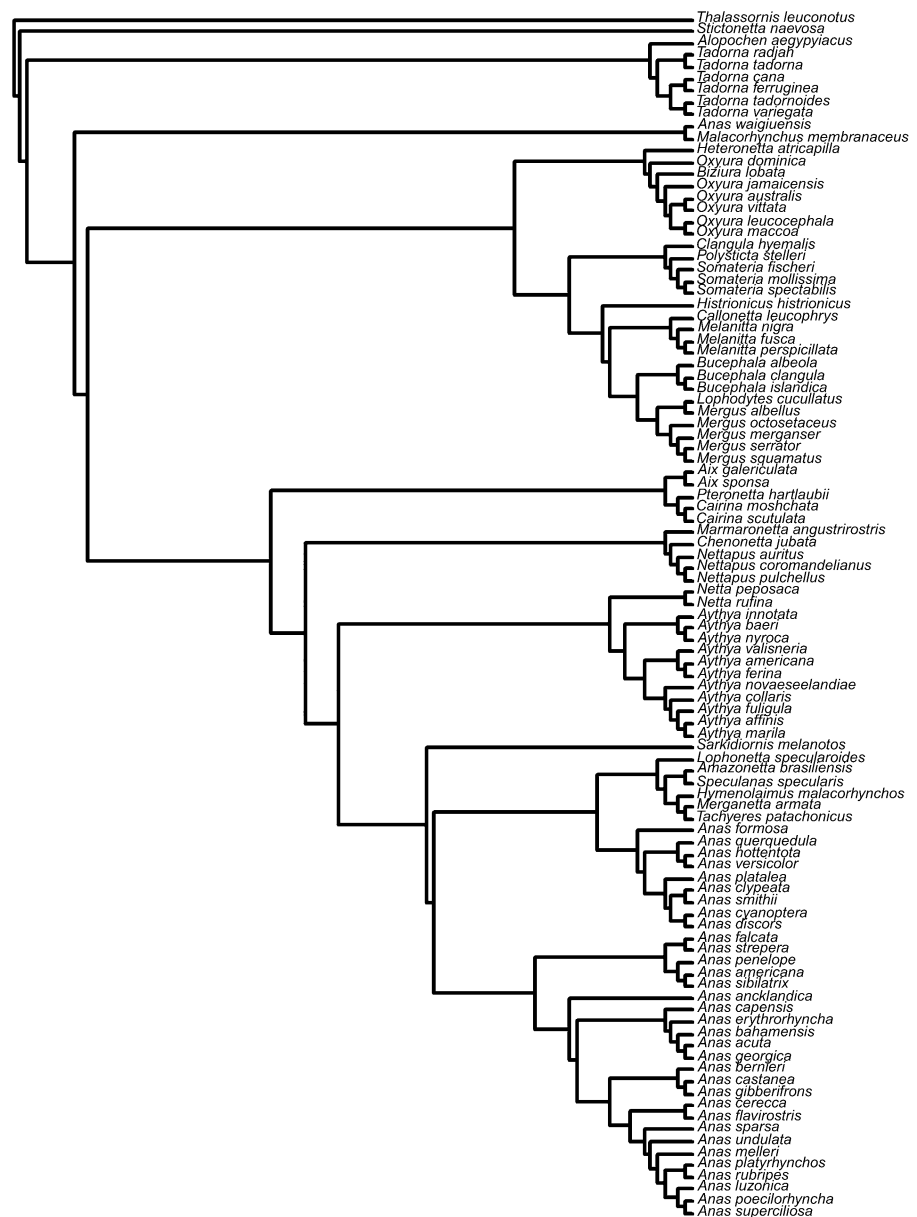


Figure 1
 The composite phylogeny of ducks (Anatinae) used in the present analyses.

the exact relatedness distances were often unknown, we used unit branch lengths (Purvis et al. 1994).

Associations between 2 continuous variables and between a discrete and a continuous variable were examined in the phylogenetic regression macro of SAS (version 0.7; Grafen 2006). This program uses the independent contrasts method (Felsenstein 1985; Harvey and Pagel 1991). Relationships between 2 binary variables were tested in Bayes discrete (Pagel and Meade 2006), using maximum likelihood estimation. Bayes discrete assumes that simultaneous changes of character state in the 2 variables do not occur. Accordingly, a test of the correlated evolution of 2 binary traits is based on a comparison of an independent model using 4 parameters (1 for each character state) with a dependent model in which 8 parameters are estimated (1 for each possible character state transition). These models are compared in a likelihood ratio test where the difference in the $-2 \times \log$ likelihood of the 2 models is distributed as χ^2 with 4 df (Pagel 1994).

Statistical tests of male covert patches, female covert patches, and covert patch dichromatism are not independent. To account for this without loss of statistical power, we report effect sizes and their confidence intervals (CIs) for every test

(Nakagawa 2004). Several explanatory variables are correlated, so we also conducted a 2-step multivariate analysis of the 3 continuous dependent variables, using generalized least squares regressions with backward stepwise selection and re-introduction in the R computing environment (Garamszegi and Møller 2007). We first tested all predictors except testis size and phallus length and then entered the latter 2 into a separate model. Despite the reduced sample sizes ($N = 89$ and $N = 22$, respectively), the effect sizes obtained were highly concordant with those found in univariate tests ($r = 0.732$, $P < 0.001$). The smaller samples impair the precision of estimates in the multivariate models, so we report the univariate results here.

RESULTS

Ecological predictors

All details of the results are shown in Table 1. The white covert patch size and the body mass of males were positively correlated (Figure 2). Flight feather patches, female covert patches, or covert patch dichromatism were unrelated to the body

Table 1
Relationships between white wing patch expression and descriptors of ecology and sexual selection in ducks

Dependent variable	Predictor	Test statistic	df	Effect (r)	CI lower	CI upper
Flight feather patch	Mating system	0.33	1, 65	0.071	-0.174	0.308
Flight feather patch	Testis size	0.03	1, 21	-0.205	-0.537	0.182
Flight feather patch	Phallus length	0.39	1, 28	-0.117	-0.464	0.261
Flight feather patch	Male mass	0.04	1, 71	-0.024	-0.254	0.209
Flight feather patch	Female mass	0.36	1, 71	-0.071	-0.298	0.163
Flight feather patch	Mass dimorphism	2.96	1, 71	0.200	-0.033	0.413
Flight feather patch	Habitat	0.31	1, 66	-0.068	-0.304	0.175
Flight feather patch	Nest site	1.63	1, 65	0.156	-0.089	0.384
Flight feather patch	Paternal care	0.07	1, 67	-0.032	-0.269	0.208
Flight feather patch	Incubation length	0.11	1, 66	-0.041	-0.278	0.201
Male covert patch	Mating system	0.52	1, 50	0.101	-0.179	0.367
Male covert patch	Testis size	0.06	1, 15	0.028	-0.356	0.403
Male covert patch	Phallus length	11.74**	1, 27	-0.550	-0.766	-0.223
Male covert patch	Male mass	4.19*	1, 58	0.260	0.004	0.484
Male covert patch	Female mass	0.64	1, 60	0.103	-0.153	0.346
Male covert patch	Mass dimorphism	2.81	1, 58	-0.215	-0.446	0.044
Male covert patch	Habitat	1.56	1, 51	0.172	-0.106	0.425
Male covert patch	Nest site	0.08	1, 50	0.040	-0.238	0.312
Male covert patch	Paternal care	1.42	1, 62	-0.150	-0.383	0.102
Male covert patch	Incubation length	1.10	1, 56	0.139	-0.126	0.385
Female covert patch	Mating system	3.34	1, 58	0.233	-0.024	0.462
Female covert patch	Testis size	0.64	1, 14	0.184	-0.219	0.534
Female covert patch	Phallus length	12.83**	1, 27	-0.568	-0.776	-0.247
Female covert patch	Male mass	0.53	1, 60	0.094	-0.162	0.337
Female covert patch	Female mass	0.24	1, 69	0.059	-0.179	0.290
Female covert patch	Mass dimorphism	1.51	1, 60	-0.157	-0.393	0.099
Female covert patch	Habitat	1.66	1, 59	0.165	-0.092	0.402
Female covert patch	Nest site	0.11	1, 58	0.044	-0.215	0.296
Female covert patch	Paternal care	8.09**	1, 66	-0.330	-0.529	-0.098
Female covert patch	Incubation length	0.41	1, 60	0.082	-0.327	0.173
Covert patch dichromatism	Mating system	<i>4.65</i>	<i>4</i>	<i>0.217</i>	<i>0.020</i>	<i>0.397</i>
Covert patch dichromatism	Testis size	0.41	1, 26	0.093	-0.234	0.400
Covert patch dichromatism	Phallus length	1.52	1, 66	0.150	-0.377	0.262
Covert patch dichromatism	Male mass	0.00	1, 96	0.000	-0.199	0.199
Covert patch dichromatism	Female mass	0.01	1, 96	0.010	-0.190	0.209
Covert patch dichromatism	Mass dimorphism	0.02	1, 96	0.014	-0.186	0.213
Covert patch dichromatism	Habitat	0.62	1, 60	0.101	-0.155	0.344
Covert patch dichromatism	Nest site	<i>4.86</i>	<i>4</i>	<i>0.221</i>	<i>0.026</i>	<i>0.400</i>
Covert patch dichromatism	Paternal care	1.33	1, 47	0.166	-0.124	0.430
Covert patch dichromatism	Incubation length	0.27	1, 85	0.056	-0.157	0.265

Results in normal font are F values calculated in the phylogenetic regression macro of SAS, with effect and error df. Results in italic are likelihood ratio χ^2 tests with 4 df, calculated using Bayes discrete. Significant patterns are shown in bold. * $P < 0.05$; ** $P < 0.01$; CI, 95% CI of effect size.

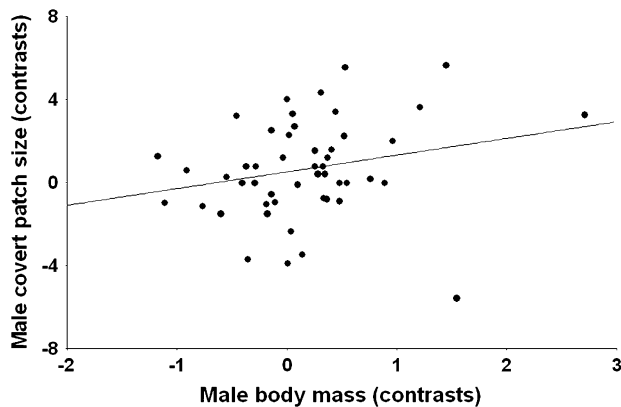


Figure 2

The size of white covert patches in male ducks in relation to their body mass: independent contrasts. Zero contrasts are not shown.

mass of either sex, and mass dimorphism did not predict white wing patch expression. White wing patch expression does not seem to have coevolved with either habitat or nest site. There was a similar lack of relationships for incubation length. However, species with higher covert patch expression in females showed lower paternal care scores, that is, female patch expression increased with the contribution of males to parental duties (Figure 3).

Sexual selection

There was no relationship between white patch expression and social mating system or testis size. Phallus length was significantly negatively related to both male and female covert patch scores (Figure 4), but the relationship was not significant for the flight feather patch or dichromatism in covert patch expression. Phallus length and testis size were significantly positively correlated ($F_{1,20} = 7.30$, $P = 0.014$, $r = 0.517$, CI lower = 0.110, CI upper = 0.776). Finally, it is possible that a correlated variable explains the relationship of one predictor with the dependent variable. However, relationships between multiple predictors of the same patch expression measure were not significant (phallus length and male mass $F_{1,38} = 0.16$, $P = 0.696$, $r = 0.065$, CI lower = -0.256 , CI upper = 0.373; paternal care and phallus length $F_{1,25} < 0.01$, $P = 0.997$, $r = 0.000$, CI lower = -0.387 , CI upper = 0.387), and 2-step multivariate models gave results similar to those shown here (see Methods).

DISCUSSION

We assessed some morphological and behavioral evolutionary correlates of white wing patch expression in ducks. Previous comparative studies of the larger group of waterfowl focused on overall plumage brightness (Scott and Clutton-Brock 1989; Figuerola and Green 2000), which allows us to make tentative comparisons between these 2 measures of conspicuousness. The size of sexually uniform flight feather patches was not related to any predictor we examined. This may be explained by the fact that these patches, unlike the covert patches, are difficult to see at rest. More surprisingly, the same lack of relationships was found for sexual dichromatism in white patches on the wing coverts. However, when considering the sexes separately, male covert patch size was positively related to body mass, whereas female covert patch size correlated positively with male contribution to parental care. The most striking result was the strong negative correlation of phallus length with both male and female covert patch expression.

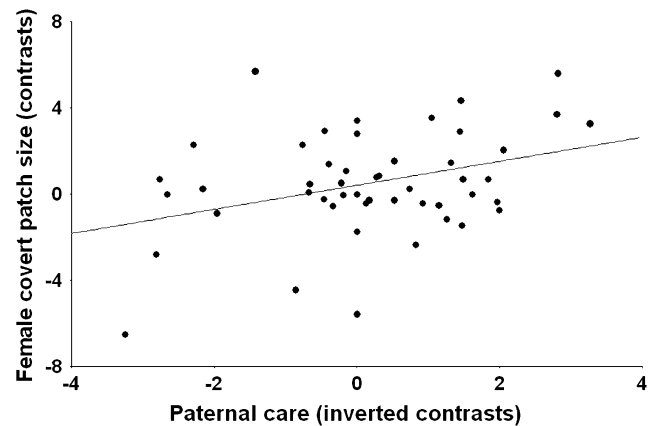


Figure 3

The size of white covert patches in female ducks in relation to male contribution to paternal care: independent contrasts. The original male paternal care scores of Scott and Clutton-Brock (1989) are negatively related to male contribution to care, so we multiplied the contrasts by -1 on this graph to facilitate understanding. Zero contrasts are not shown.

Ecological predictors of white wing patches

White patches have 2 specific characteristics that lend special importance to the ecological predictors we examined here. First, the lack of melanin from extended regions on the flight

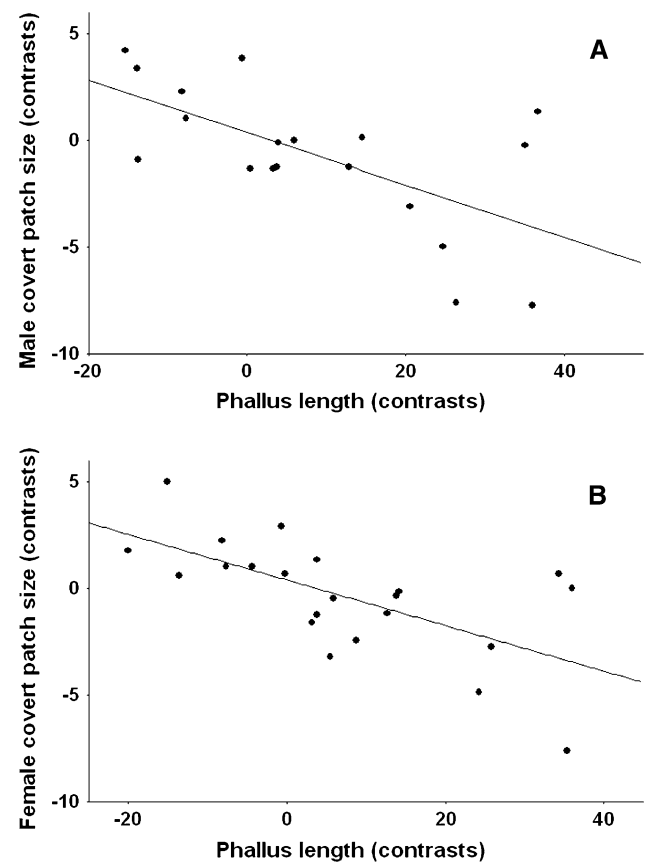


Figure 4

Relationships between male phallus length and the size of white covert patches on (A) males and (B) females: independent contrasts. Zero contrasts are not shown.

feathers may lead to abrasion and breakage (Bonser 1995; Kose and Møller 1999), which in turn increases flight costs (Swaddle et al. 1996). Second, contrasting white patches are particularly conspicuous (Slagsvold et al. 1995; Jabłoński et al. 2006), and this applies irrespective of visual system because white plumage patches are nearly always monochromatic bright also in the UV range (Eaton and Lanyon 2003). The conspicuousness of white patches may make their evolution particularly sensitive to any factor related to visibility or communication. This fact links much of the ecological predictors discussed below.

Body mass is expected to coevolve with white wing patches for 3 reasons. First, body size is often itself an indicator of sexual selection intensity and it may therefore correlate with ornamentation (Höglund 1989; Webster 1992). Second, the mechanical costs of white wing patch expression on the flight feathers, but not the coverts, may be related to body size (Hedenström 1993; Harrison and Roberts 2000). Finally, body size and the corresponding wing size may affect the visibility distance of patterns on the wing, influencing their evolution. We found that the size of flight feather patches was unrelated to body mass, which does not support the mechanical cost hypothesis. However, covert patch size was positively related to body mass in males but not in females. These relationships suggest a special joint role for covert patches and body mass in males. One such role could be sexual competition, which simultaneously facilitates the evolution of body mass and white covert patches as indicators of quality, leading to a positive evolutionary correlation between mass and patch expression. Indeed, sexual competition is much stronger among male ducks than among females (McKinney et al. 1983; Johnson 2000).

The parental activities of females, particularly incubation, may increase the wearing costs of conspicuous traits (Baker and Parker 1979; Martin and Badyaev 1996), although direct positive selection on female ornamentation, for example in terms of resource defense, may counterbalance these costs (Bleiweiss 1985; Trail 1990; Whittingham et al. 1992). Several studies have shown reductions in female conspicuousness in species with more exposed nest sites (Johnson 1991; Martin and Badyaev 1996; Dunn et al. 2001), whereas other studies have emphasized the negative relationship between female trait expression and the length of the incubation period (Badyaev 1997; Bókony and Liker 2005). Hole nesting may reduce viability selection against conspicuousness, but it may increase competition because of the limited availability of nest cavities (Scott and Clutton-Brock 1989; Newton 1994; Kraaijeveld 2003). Finally, habitat features may also modify the optimal visual signaling strategy (Endler 1993; Johnson and Lanyon 2000). Wavelength-specific effects of habitats on plumage color seem generally clear-cut (Endler and Théry 1996; McNaught and Owens 2002; Gomez and Théry 2004). However, the patterns of monochromatic brightness and contrast, also represented by white patches, are controversial (Marchetti 1993; McNaught and Owens 2002). Our data showed no relationship between the expression or dichromatism of conspicuous white wing patches (Brooke 1998; Jabłoński et al. 2006) and incubation length, nest site, or habitat openness. These results uniformly reject predation as a factor shaping differences in white wing patterns among duck species (also see Figuerola and Green 2000). Wing patches occupy only a small percentage of the visible surface of the animal, and their consequences to conspicuousness may be swamped by the overall brightness and large seasonal changes of the entire plumage (Madge and Burn 1987; Pyle 2005).

In addition to predation, investment in reproduction may trade-off with mating opportunities (Kirkpatrick and Ryan 1991; Fitzpatrick et al. 1995) and hormonal mechanisms may also cause a negative evolutionary relationship between

mating investment and paternal care (Ketterson et al. 1992; Garamszegi et al. 2005). In contrast to the results of Scott and Clutton-Brock (1989) for brightness, we found that paternal care was not associated with white patch dichromatism on the wing coverts. However, female (but not male) covert patch size showed a positive correlation with paternal care contribution. Female patches may become more important in species where more male care is needed due to a harsh environment that necessitates biparental care. In this case, the significance of female care is also increased, accompanied by a need for quality indication (Lack 1968; Temrin and Sillén-Tullberg 1994). Alternatively, males may prove choosier when their contribution is more limiting (Johnstone et al. 1996). Finally, if females perform most parental duties alone, they may have less opportunity for sexual advertisement (Parker and Simmons 1996). Note that brood amalgamation in some duck species may complicate the interpretation of parental investment data (Öst et al. 2002). To conclude, several ecological correlates emerged for white covert patches but no predictor correlated with white patch expression on the flight feathers, and variables reflecting the wearing costs of conspicuous traits did not predict the evolution of white wing patches. Further studies are needed to elucidate the evolutionary forces that maintain white flight feather patches in ducks (Brooke 1998) and the factors that limit the expression of white wing patches in this group (Kirkpatrick and Ryan 1991; Slagsvold et al. 1995; Martin and Badyaev 1996).

White wing patches and sexual selection

When evaluating the evolutionary relationships between sexual selection and white wing patch expression in ducks, we applied both the traditional approach using sexual dichromatism as a measure of sexual selection (e.g., Gray 1996; Badyaev and Hill 2000; Johnson 2000) and independent evaluations of trait expression in both sexes, irrespective of dichromatism (e.g., Bókony et al. 2003; Hausmann et al. 2003; Kraaijeveld 2003; Bókony and Liker 2005). The latter approach is important because the speed of the evolution of female ornamentation may exceed that of male ornamentation (Irwin 1994; Burns 1998; Wiens 2001), and monochromatic brightness may be functionally highly meaningful (e.g., Trail 1990; Whittingham et al. 1992; Jones and Hunter 1998).

White wing patterns in ducks are sexually monochromatic in the majority of species. Indeed, we were able to detect sex differences in the expression of flight feather patches in only a single species, although dichromatism was more frequent in covert patches. Moreover, wing patches are visible all year round, in contrast to coloration on the rest of the body (Madge and Burn 1987). Therefore, selection pressures on white wing patches may differ from those shaping overall plumage brightness (e.g., Scott and Clutton-Brock 1989; Figuerola and Green 2000).

Ducks are overwhelmingly monogamous, so we quantified sexual selection in terms of social mating system as the frequency of mate change (Scott and Clutton-Brock 1989; for a similar approach, see Kraaijeveld 2003). A previous study of waterfowl found that mating frequency positively predicted overall sexual dichromatism (Scott and Clutton-Brock 1989). Our data on the white wing patches of ducks showed no such pattern. The lack of significant pattern is especially striking for female covert patches ($P = 0.073$) because these are significantly related to paternal care, a variable that shows very strong correlated evolution with mating frequency ($P < 0.001$ in our data set). Our results therefore suggest that the main sexual selection role of the white wing patches of ducks is in processes other than social mate choice, for example, in social competition, intrasexual contests, differential allocation, or sperm competition.

We considered sperm competition from 2 points of view. Whereas testis size is a general descriptor of sexual selection by sperm competition (Møller and Briskie 1995), phallus length has recently been associated specifically with forced copulations (Coker et al. 2002), a behavior common in waterfowl, but rare in other birds (McKinney et al. 1983). Forced copulations involve at least 2 evolutionary conflicts: a race among males over mating, manifested in a positive correlation between testis size and phallus length (Coker et al. 2002), and an arms race between the female and the male, manifested in a positive correlation between the 2 sexes in the complexity of their genital tracts (Brennan et al. 2007). We found no relationship between white wing patches and testis size but very strong negative correlations between the sizes of both male and female covert patches and phallus length. The incongruence of patterns for testis size and phallus length is particularly interesting because the 2 traits show positive coevolution (Coker et al. 2002), which is detectable even in our small set of data. The correlation between phallus length and testis size also suggests that the lack of relationship between white patch expression and testis size was not due to the poor quality of the testis size data set (Calhim and Birkhead 2007).

The correlation between phallus length and male covert patch size may suggest that male advertisement is less important or even disadvantageous in species where most copulations are forced. Males, if less conspicuous, may get closer to the female before being noticed, and this may increase the probability of a successful forced copulation (McKinney et al. 1983). Alternatively, male wing patches may successfully function as signals during mate defense from forced copulations, in which case males of species without mate defense may have smaller white patches and more copulations than those with defense (Gowaty and Buschhaus 1998). The negative correlation between male phallus length and female covert patch expression, on the other hand, could reflect the lack of need for indicators of female quality where males are successful in achieving mating by force. However, this explanation may not hold because forced copulations do not uniformly increase the reproductive success of males (Gowaty and Buschhaus 1998; Brennan et al. 2007). More empirical data are needed on the role of visual communication during extrapair copulations in ducks, with a particular emphasis on female signals (Cunningham 2003; Lazarus et al. 2004). Studies within each species should clarify the phenotypic variability and quality indicator value of white patch expression (Hanssen et al. 2006) as well as its function in sexual selection (Omland 1996a, 1996b), including forced copulations (Gowaty and Buschhaus 1998).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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